

# MAASTRICHTIAN NON-HETEROMORPH AMMONITES FROM THE MIRIA FORMATION, WESTERN AUSTRALIA

by R. A. HENDERSON and K. J. MCNAMARA

**ABSTRACT.** Twenty-two species of non-heteromorph ammonites, distributed among fourteen genera, are described from the Miria Formation, Western Australia. The species *Kitchinites spathi*, *Gunnarites raggatti*, *Kossmaticeras* (*Natalites*) *brunnschweikeri*, *Neograhamites carnarvonensis*, and *Brahmaites* (*Brahmaites*) *kossmati*, and the subspecies *Pachydiscus* (*Pachydiscus*) *neubergicus dissitus* and *P. (P.) jacquoti australis* are described as new. *Pachydiscus* species shared with Western Europe date the Miria Formation as Maastrichtian, consistent with its age assignment based on Foraminifera. The Kossmaticeratidae is the most diverse family, contributing more than a third of the species. Maastrichtian records for the kossmaticeratid genera *Gunnarites*, *Maorites*, *Kossmaticeras* (*Natalites*), *Grossouvrites*, and *Neograhamites*, which previously had been thought to range no higher than Campanian, are new. The age attributable to the Miria Formation ammonite assemblage is reviewed in relation to standard Maastrichtian ammonite faunas from Western Europe.

THE Miria Formation (Miria Marl of Condon *et al.* 1956) occurs as a thin unit in the Cretaceous succession of the Giralda Anticline, which forms the Giralda Range, lying to the south of Exmouth Gulf, Western Australia. It consists of cream calcarenite 0.6–2.0 m thick, underlain by the Korojon Calcarenite and disconformably succeeded by the Palaeocene Boongerooda Greensand. Phosphatic grains and nodules are locally abundant and much of the rich fossil complement of the Miria Formation occurs as phosphatic moulds. Stream dissection of the western and north-eastern flanks of the Giralda Range provide the principal exposures of the Miria Formation. Here the unit is abundantly fossiliferous over a strike-length of about 80 km (text-fig. 1).

A rich fauna is present in the Miria Formation. In addition to ammonites, it includes a diverse assemblage of Foraminifera (Edgell 1957; Belford 1958), the nautiloid *Cimomia tenuicostata* Glenister, Miller and Furnish (1956) and a number of undescribed brachiopods, corals, echinoids, sponges, bryozoans, and shark teeth. Unpublished work by Darragh and Kendrick (pers. comm.) has revealed an assemblage of over sixty species of gastropods and bivalves.

The ammonites are especially noteworthy. Existing collections contain over 1500 specimens and constitute the most abundant assemblage of Maastrichtian ammonites as yet recorded. The assemblage is thus highly relevant to any assessment of the abundance and diversity of ammonites immediately prior to their demise at the end of the Cretaceous Period.

Early reports of the Miria Formation by Condit (1935) and Raggatt (1936) noted its fossiliferous nature and a collection of ammonites was examined by Whitehouse (*in* Raggatt 1936). A number of ammonites collected by C. Teichert in 1938 were described by Spath (1941), who recorded eight species of non-heteromorph ammonites: *Paraphylloceras* aff. *vera* (Forbes), *Phyllopacllyceras forbesianum* (d'Orbigny), *Pseudophyllites* cf. *indra* (Forbes), *Hauericeras durga* (Forbes), *Kossmaticeras* sp. nov.? aff. *aemilianus* (Stoliczka), ?*Kitchinites* sp. indet., *Pachydiscus gollevillensis* (d'Orbigny), and *Pachydiscus* sp. nov.? cf. *grossouvrei* Kossmat. Spath, following Raggatt, erroneously described the ammonites as coming from 'glauconitic sand to sandstone'. The unit to which they refer is the overlying Boongerooda Greensand. This error no doubt arose from the way in which the ammonites occur, eroded out and scattered on the ground surface.

Brunnschweiler (1966), in describing the heteromorph ammonite fauna of the Miria Formation, favoured a late Cretaceous age for the Boongerooda Greensand, on account of the rare occurrence of ammonites. We have also collected ammonites from the base of the Boongerooda Greensand, but they are often worn and invariably have glauconitic and phosphatic coatings. We regard them as having been reworked from the underlying Miria Formation. An early Palaeocene (planktonic Foraminiferal Zone 2) age attributed to the Boongerooda Greensand by McGowran (1968, 1978) supports this view and indicates a disconformable relationship between it and the Miria Formation.

Spath (1941) suggested an early Maastrichtian age for the ammonites he examined. Brunn-schweiler (1966), however, considered that the heteromorph ammonite fauna was of late Campanian to early Maastrichtian age. The collection in recent years of a large number of specimens has allowed us to present this first embracing description of the non-heteromorph ammonites and to reassess the age of the fauna.

We will be revising the heteromorph ammonite fauna in a forthcoming paper. The descriptions are based primarily on three major collections: one made by G. Kendrick and T. Darragh in 1969, another by K.J.M. with Kendrick and Darragh in 1979, and the third by the same group plus R.A.H. in 1983. These collections are housed in the Western Australian Museum (WAM) and the Museum of Victoria (NMV). We have also made use of Teichert's 1938 collection, which is housed in the Department of Geology, University of Western Australia (UWA). Other specimens examined and referred to in the text are from collections in the British Museum, Natural History (BM), and the Oxford University Museum (OUM).

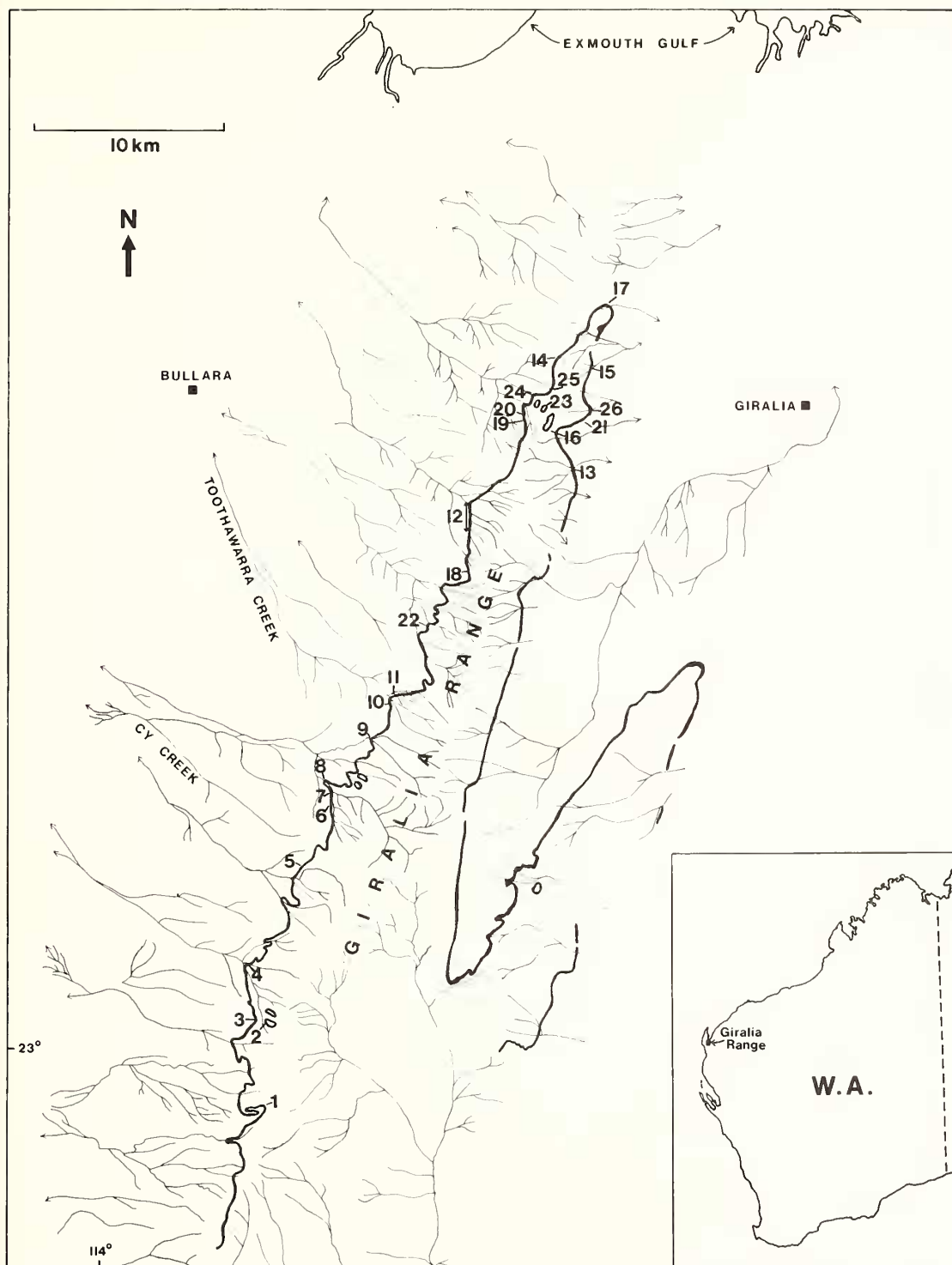
The positions of the twenty-six localities, which provided the collections on which this paper is based, are shown in text-fig. 1 and listed below.

1. Remarkable Hill, Cardabia Station (KV 013502). 2. Section Hill, Cardabia Station (KV 017543). 3. 500 m west of Section Hill, Cardabia Station (KV 012543). 4. 3.5 km north-north-west of Section Hill, Cardabia Station (JV 997579). 5. Creek, 6.5 km east of no. 10 bore, Cardabia Station (KV 026630). 6. Southern tributary of CY Creek, Cardabia Station (KV 044657). 7. CY Creek, Cardabia Station (KV 044667). 8. CY Creek, Cardabia Station, 2–3 km east of no. 37 bore (KV 038679). 9. Northern tributary of CY Creek, Cardabia Station (KV 070708). 10. Southern tributary of Toothawarra Creek, Cardabia Station (KV 069722). 11. Type section of the Miria Formation, Toothawarra Creek, Cardabia Station (KV 070725). 12. 3–6 km north-north-west of Whitlock Dam, Giralia Station (KV 115812–115832). 13. 7 km west-south-west of Deep Well, Giralia Station (KV 160832). 14. East side of Walatharra Paddock, Giralia Station (KV 169912). 15. 12 km west of Giralia Homestead, Giralia Station (KV 180910). 16. 2.3 km west-south-west of West Tank, Giralia Station (KV 160870). 17. 6 km south of Centipede Hill, Giralia Station (KV 180945). 18. 2 km west-north-west of Whitlock Dam, Giralia Station (KV 116789). 19. 4 km west-south-west of West Tank, Giralia Station (KV 143872). 20. 4 km west-north-west of West Tank, Giralia Station (KV 145880). 21. 1 km west-north-west of West Tank, Giralia Station (KV 174880). 22. 5 km west-south-west of Whitlock Dam, Bullara Station (KV 090770). 23. 2.5 km north-west of West Tank, Giralia Station (KV 159885). 24. 3.5 km north-west of West Tank, Giralia Station (KV 150890). 25. 3 km north-west of West Tank, Giralia Station (KV 160895). 26. 1 km north-west of West Tank, Giralia Station (KV 175883).

All grid references refer to the Giralia 1:100 000 topographic map, except for locality 1, which is on the adjacent Mia Mia 1:100 000 sheet.

#### SYSTEMATIC PALAEOLOGY

Morphological terms are from Arkell *et al.* (1957), except those applied to elements of the suture, which are from Wedekind (1916, see Kullman and Wiedmann 1970), and to the septal surface of the *Lytocera*ta, which are from Henderson (1984). Synonymy lists are selective and contain only important revisions, significant recent citations, and new additions. Dimensions are in millimetres and the following abbreviations are employed: D, shell diameter; H whorl height; B, whorl breadth; B/H, whorl breadth/height ratio; U, umbilical diameter; %, umbilical diameter as a percentage of the shell diameter.



TEXT-FIG. 1. Locality map showing the distribution of the Miria Formation and the location of sites from which collections have been made. Outcrop data based on Condon *et al.* (1956).

Suborder PHYLLOCERATINA Arkell, 1950  
 Family PHYLLOCERATIDAE Zittel, 1884  
 Subfamily PHYLLOCERATINAE Zittel, 1884  
 Genus PHYLLOCERAS Suess, 1865  
 Subgenus NEOPHYLLOCERAS Shimizu, 1934

- 1934 *Neophylloceras* Shimizu, p. 61.  
 1935 *Paraphylloceras* Shimizu (*non* Salfeld, 1919), p. 180.  
 1947 *Hyporbulites* Breistroffer, p. 82.  
 1956 *Epiphyllloceras* Collignon, p. 24.

*Type species.* *Ammonites* (*Scaphites*?) *ramosus* Meek, 1857.

*Diagnosis.* Moderately to strongly compressed, strongly involute shells retaining a small open umbilicus and ornamented with thin, closely spaced, radial or weakly flexuous lirae. Additional ornament of radial costae, or indistinct, broad folds or narrow, shallow grooves may be present on the dorsal flanks. Suture complexly divided with small, indistinctly tetraphylloid terminations to saddles margining the lateral lobe.

*Remarks.* *Neophylloceras* was introduced by Shimizu (1934) in an obscure publication and was largely ignored until Wright and Matsumoto (1954) reviewed its status and confirmed its validity. Subsequently its usefulness has been much debated. It was treated as a junior subjective synonym of *Hypophylloceras* Salfeld, 1924 by Arkell, Kummel and Wright (1957), Wiedmann (1962a), Wiedmann and Dieni (1968), and Kennedy and Klinger (1977a). However, Usher (1952), Matsumoto (1959a, b), Packard (1960), Jones (1963), and Henderson (1970) all considered *Neophylloceras* as distinct by virtue of its more complex suture with less pronounced phylloid terminations to the saddles when compared with *Hypophylloceras*. Birkelund (1965) and Matsumoto and Morozumi (1980) thought that *Neophylloceras* was best placed as a subgenus of *Hypophylloceras*.

Wiedmann (1962a, b) drew attention to the very slow evolution of Jurassic and early Cretaceous *Phylloceras* and its Cretaceous derivative stocks whereby Jurassic representatives are separated from those of late Cretaceous age by rather small morphological differences. This had resulted in the introduction of a plethora of generic categories into the literature to represent very small changes in morphology, for reasons of biostratigraphic propriety rather than those of objective systematics.

The only characteristic which serves to distinguish Jurassic *Phylloceras* from their Cretaceous descendants is the nature of the suture. It is relatively simple, with large biphylloid or triphylloid terminal elements to the saddles in Jurassic species, of which the type species *P. heterophyllum* (Sowerby) is a typical representative, and becomes much more complex with small, almost unrecognizable, tetraphylloid terminations to the saddles in late Cretaceous forms (text-fig. 2). When the complete array of species is considered, all gradations in sutural type are evident (text-fig. 2) and natural breaks in the range of morphology are not readily apparent.

There are, however, three clusters of species which may be recognized on the basis of sutural morphology and into which the great majority of species can be readily fitted. Generic categories are already well established for all three: *Phylloceras* Suess (*s.s.*), type species *P. heterophyllum* (Sowerby); *Hypophylloceras* Salfeld, type species *H. onoense* (Stanton); and *Neophylloceras* Shimizu, type species *N. ramosum* (Meek). Even though the two end-members, *Phylloceras* (*s.s.*) and *Neophylloceras*, are quite separate in sutural character, subgeneric status is here considered to be the most satisfactory way of expressing relationships within the *Phylloceras* (*s.s.*)-*Hypophylloceras*-*Neophylloceras* plexus. Following Matsumoto (1959a) *P. seresitense* Pervinquier, which is intermediate between *P. (H.) onoense* and *P. (N.) ramosum* in terms of its suture, is included in *Neophylloceras*. *Hyporbulites* Breistroffer, with *P. (N.) seresitense* as its type species, thereby becomes a junior subjective synonym of *Neophylloceras*.





TEXT-FIG. 2. *a-c*, sutural discrimination of subgenera within *Phylloceras*. *a*, type species of *Phylloceras* (*Phylloceras*), *P. (P.) heterophyllum* (J. Sowerby), OUM J17844, Toarcian,  $\times 1\frac{1}{2}$ ; *b*, type species of *Phylloceras* (*Hypophylloceras*), *P. (H.) onoense* (Stanton), from Matsumoto 1959*a*, text-fig. 5, lower Cretaceous (precise age uncertain),  $\times 1\frac{1}{2}$ ; *c*, type species of *Phylloceras* (*Neophylloceras*), *P. (N.) ramosum* (Meek), from Jones 1965, text-fig. 7, upper Campanian or lower Maastrichtian,  $\times 1\frac{1}{2}$ . *d-g*, sutures of *Phylloceras* (*Neophylloceras*). *d*, *P. (N.) sersitense* (Pervinquiere) from Matsumoto 1959*a*, text-fig. 3, upper Albian or Cenomanian,  $\times 3$ ; *e*, *P. (N.) hetonaiense* Matsumoto, from Jones 1963, text-fig. 8, upper Campanian or lower Maastrichtian,  $\times 1.25$ ; *f*, *P. (N.) groenlandicum* Birkelund, from Birkelund 1965, text-fig. 8, Maastrichtian,  $\times 3.5$ ; *g*, *P. (N.) surya* (Forbes), WAM 81.2409, lower Maastrichtian,  $\times 2.5$ .

Phylloceras (Neophylloceras) as thus defined ranges from the Albian to the Maastrichtian and includes some twenty nominate species among which there are doubtless a substantial number of synonyms. *Epiphyllloceras* Collignon 1956 (type species *Ammonites surya* Forbes) has been consistently treated as a synonym of *Neophylloceras*. *Paraphylloceras* Shimizu 1935, also introduced for *A. surya* Forbes and its allies, is a stillborn homonym of *Paraphylloceras* Salfeld 1919 (see Wright and Matsumoto 1954). *A. surya* is redescribed herein and the widely held view that it is best considered a *Neophylloceras* is re-endorsed.

*Phylloceras* (*Neophylloceras*) *ramosum* (Meek, 1857)

Plate 1, figs. 1–3; text-fig. 2c

1857 *Annonites* (*Scaphites*?) *ramosus* Meek, p. 45.

1970 *Neophylloceras ramosum* (Meek); Henderson, p. 5, pl. 1; fig. 3, text-fig. 2a.

1980 *Hypophylloceras ramosum* (Meek); Blasco *et al.*, p. 477, pl. 2, figs. 1–4.

*Material.* Four specimens, localities 12, 15, 18, and 23.

*Description.* Shell discoidal and strongly involute, the umbilicus measuring some 8.5% of the shell diameter. Whorls approximately twice as wide as high, very weakly convex, their axis of maximum width a little dorsal of the mid-flank. Umbilical wall steep, curving smoothly into the flank, without an abrupt shoulder. Flanks only very slightly convergent so that the venter is quite broadly arched for such a compressed shell. Ornament of fine, closely spaced lirae numbering approximately 125–150 in a half whorl, becoming slightly more numerous with growth. Lirae are not preserved on the dorsal flanks; they are retradiate on the ventral flanks and weakly projected across the venter. Suture complexly divided with auxiliary elements of the umbilical lobe arrayed in a radial line.

*Dimensions.*

	D	H	B	B/H	U	%
WAM 80.968	41.0	23.5	12.0	0.51	3.5	9

*Remarks.* *P. (N.) ramosum* is widely distributed on the borderlands of the Pacific Ocean, having been recorded from Alaska, Vancouver Island, California, southern South America, the Antarctic Peninsula, New Zealand, and Japan. However, nowhere is it represented by a substantial suite of specimens allowing proper documentation of its intraspecific variation. In consequence, its relationships to other nominate species of *Phylloceras* (*Neophylloceras*) are somewhat conjectural. It is closely related to *P. (N.) hetonaiense* Matsumoto (redescribed by Matsumoto 1959*b* and Jones 1963) (= *P. (N.) lambertense* Usher, 1952) and to *P. (N.) woodi* (van Hoepen, 1921) (redescribed by Kennedy and Klinger 1977*a*) (= *Hyporbulites hoeperi* Collignon, 1956). A distinction from these two species appears to be provided by its more compressed whorl profile, at least in the early growth stages to a shell diameter of some 50 mm, and by more flexuous lirae. Its distinction from the Indian *P. (N.) nera* (Forbes) is less convincing and depends solely on the lirae which are less flexuous in the Indian species and not projected on the venter.

EXPLANATION OF PLATE I

Figs. 1–3. *Phylloceras* (*Neophylloceras*) *ramosum* (Meek), WAM 80.968,  $\times 1$ .

Figs. 4–6. *Partschiceras* (*Phyllopachyceras*) *forbesianum* (d'Orbigny), WAM 80.965,  $\times 1$ .

Figs. 7–8, 11–12. *Phylloceras* (*Neophylloceras*) *surya* (Forbes). 7–8, NMV P31021. 11–12, WAM 82.3081,  $\times 1$ .

Figs. 9–10. *Anagaudryceras politissimum* (Kossmat), WAM 80.986,  $\times 1$ .

Figs. 13–14. *Gaudryceras kayei* (Forbes), WAM 80.989,  $\times 1$ .





*Phylloceras (Neophylloceras) surya* (Forbes, 1846)

Plate 1, figs. 7, 8, 11, 12; Plate 2, figs. 1, 2; text-fig. 2g

- 1846 *Ammonites surya* Forbes, p. 106, pl. 7, fig. 10a, b.  
 1941 *Paraphylloceras* sp. cf. *nera* (Forbes); Spath, p. 42.  
 1956 *Epiphyllloceras mikobokense* Collignon, p. 24, pl. 2, fig. 3, 3a; pl. 4, fig. 5, 5a, b.  
 1971 *Epiphyllloceras mikobokense* Collignon; Collignon, p. 1, pl. 640, fig. 2359.  
 1971 *Epiphyllloceras geczyi* Collignon, p. 1, pl. 640, fig. 2360.  
 1977a *Phylloceras* (*Hypophylloceras*) *mikobokense* (Collignon); Kennedy and Klinger, p. 368, pl. 12, fig. 1a, b.

*Material.* Forty-two specimens, localities 4-7, 9-13, 15-20, and 25.

*Description.* Shell discoidal and involute with an umbilicus measuring 8-11% of the shell diameter. Whorls compressed, about twice as high as wide. Umbilical wall vertical at the umbilical seam but curves outward, passing smoothly across the umbilical shoulder into the flanks which are weakly convex and converge to a narrowly rounded venter. Axis of maximum whorl breadth lies on the dorsal flanks, close to the umbilical shoulder. Ornament is of two orders. Fine, closely spaced striae separated by interspaces as wide as themselves, begin on the dorsal flanks. They are initially prorsiradiate but straighten in the mid-flank region to become almost rectiradiate. On some shells they curve slightly forward again across the venter and are thus rendered very weakly flexuous, but on others they pass straight across the venter. Striae number some sixty-five to eighty-eight per half whorl on shells 40-60 mm in diameter, but become more closely spaced relative to the shell diameter with growth so that large shells about 120 mm in diameter have 115-135 striae on the last half whorl. Well-spaced costae number twelve to fifteen per half whorl, many beginning from the umbilical shoulder, others intercalated on the dorsal flanks, reaching to the edge of the venter or almost so. On some shells they are distinctly prorsiradiate on the dorsal flanks, becoming rectiradiate in the mid-flank region; on others they are straight and rectiradiate or slightly prorsiradiate throughout. Suture very finely dissected with auxiliary elements of the umbilical lobe arrayed in a rectiradiate line.

*Dimensions.*

	D	H	B	B/H	U	%
Lectotype: BM C51075	36.5	20.0	11.0	0.55	3.5	10
NMV P31021	61.5	33.0	17.5	0.53	7.0	11
WAM 80.780	118.0	66.0	35.0	0.53	11.0	9

*Remarks.* Even though the Western Australian specimens consist mainly of whorl fragments, they are sufficient to show that the ornament is quite variable. Shells at the same growth stage show different densities of striation and strengths of costation; in addition, the curvature of both orders of ribs differs noticeably between specimens.

Six specimens of *P. (N.) surya* from Pondicherry, Southern India, including Forbes's type series, are held by the British Museum (Natural History). BM C51075 was figured by Forbes (1846, pl. 7, fig. 10a, b) and C51074 by Kossmat (1895, pl. 16, fig. 1a-c). They likewise show the ornament to be variable. The largest specimen, that figured by Kossmat, has some ninety-five striae on the last half whorl at a shell diameter of some 120 mm. It is thus more sparsely striate than any of the Western Australian specimens of comparable size. Two smaller specimens, with shell diameters of about 40 mm, have some fifty-five and sixty-five striae respectively, on their last half whorls, overlapping with the western Australian suite in this characteristic.

*P. (N.) mikobokense* (Collignon, 1956) lies within the range of variation of *P. (N.) surya* and is synonymous with it. *P. (N.) geczyi* (Collignon, 1971) is also considered to be a junior synonym. It was differentiated because of its more flexuous striae and sparse, irregular costae. Its striation appears to fall within the range of variation shown by the Pondicherry suite in the British Museum (Natural History) and by Western Australian *P. (N.) surya*. Its costation does not differ greatly from that shown by the specimen of *P. (N.) surya* figured by Stoliczka (1865, p. 115, pl. 58, fig. 5).

Two other species have ornament comparable with that of *P. (N.) surya*. They are *P. (N.) radium* (Marshall, 1926, p. 135, pl. 19, fig. 6; pl. 26, figs. 3, 4) which is of doubtful status because its type



series has been lost (Henderson 1970, p. 6), and *P. (N.) cottreani* (Collignon, 1956, p. 25, pl. 4, fig. 6, 6a). Both of these species differ from *P. (N.) surya* in having more inflated whorls and *P. (N.) cottreani* has, in addition, a much wider umbilicus.

Genus PARTSCHICERAS Fucini, 1920  
Subgenus PHYLLOPACHYCERAS Spath, 1927

1927 *Phyllopachyceras* Spath, p. 36

*Type species. Ammonites infundibulum* d'Orbigny, 1841.

*Diagnosis.* Phylloceratidae with inflated whorls varying from somewhat compressed with an oval profile to equidimensional with a rounded profile. Umbilicus a minute pit measuring 4% or less of the shell diameter. Post-juvenile shell with broad ribs continuous across the venter. Suture with L and E of equal depth or nearly so.

*Remarks.* *Phyllopachyceras* Spath (1927) was introduced without a clear diagnosis but has been adopted by many authors (Roman 1938; Drushchits 1956; Arkell, Kummel and Wright 1957; Jones 1963) to include inflated, very narrowly umbilicate phylloceratids with coarse ribs appearing on post-juvenile growth stages. Such forms were considered to be exclusively of Cretaceous age. The type species of *Phyllopachyceras*, the Barremian *P. infundibulum* (d'Orbigny), has a whorl breadth/whorl height ratio of 0.65–0.88 (Wiedmann 1964, p. 241) and is perhaps the most compressed member of the group.

Wiedmann (1964) regarded *Phyllopachyceras* as a junior subjective synonym of the Jurassic genus *Partschiceras* Fucini (1920, p. 95) on the basis that species of these two taxa form a morphological continuum. However, the type species of *Partschiceras*, subsequently designated as *P. partschi* Stur by Spath (1927, p. 38), differs from *Phyllopachyceras infundibulum* and its allies in several characteristics. It has been described by a number of authors (see Kovacs 1942 for a synonymy listing) and has a compressed whorl profile (B/H 0.5–0.63) with rather flattened flanks, an umbilicus which measures 8–14% of the shell diameter, and conspicuous constrictions on its juvenile shell. In addition, its suture has L much deeper than E. Indeed *Partschiceras* differs from *Phylloceras* (s.l.) only in post-juvenile ornament and was introduced as a subgenus of *Phylloceras* by Fucini (1920), a view which has been followed subsequently by some authors (Kovacs 1942; Sturani 1966).

*Phyllopachyceras* is here provisionally regarded as a subgenus of *Partschiceras* (s.l.), its members distinguished by the relative depth of the external lobe of the suture (text-fig. 3) and the possession of a minute umbilicus. A more compressed whorl profile serves to distinguish many *Partschiceras* (s.s.) from *Phyllopachyceras* but there is overlap in this characteristic. The oldest *Phyllopachyceras* is considered to be the Valanginian species *P. rogersi* (Kitchin, 1908, p. 179, pl. 8, fig. 19, 19a–c; see also Collignon 1962, p. 20, pl. 181, figs. 815, 816 and Cooper 1981, p. 155) which has an external lobe of characteristic form but a much wider umbilicus than typical of the subgenus. The youngest is *P. (P.) forbesianum* (d'Orbigny) which ranges into the Maastrichtian in Western Australia and elsewhere. In all, the subgenus includes some nineteen species. *Partschiceras* (s.s.) is restricted to the Jurassic.

*Partschiceras (Phyllopachyceras) forbesianum* (d'Orbigny, 1850)

Plate 1, figs. 4–6; text-fig. 3f

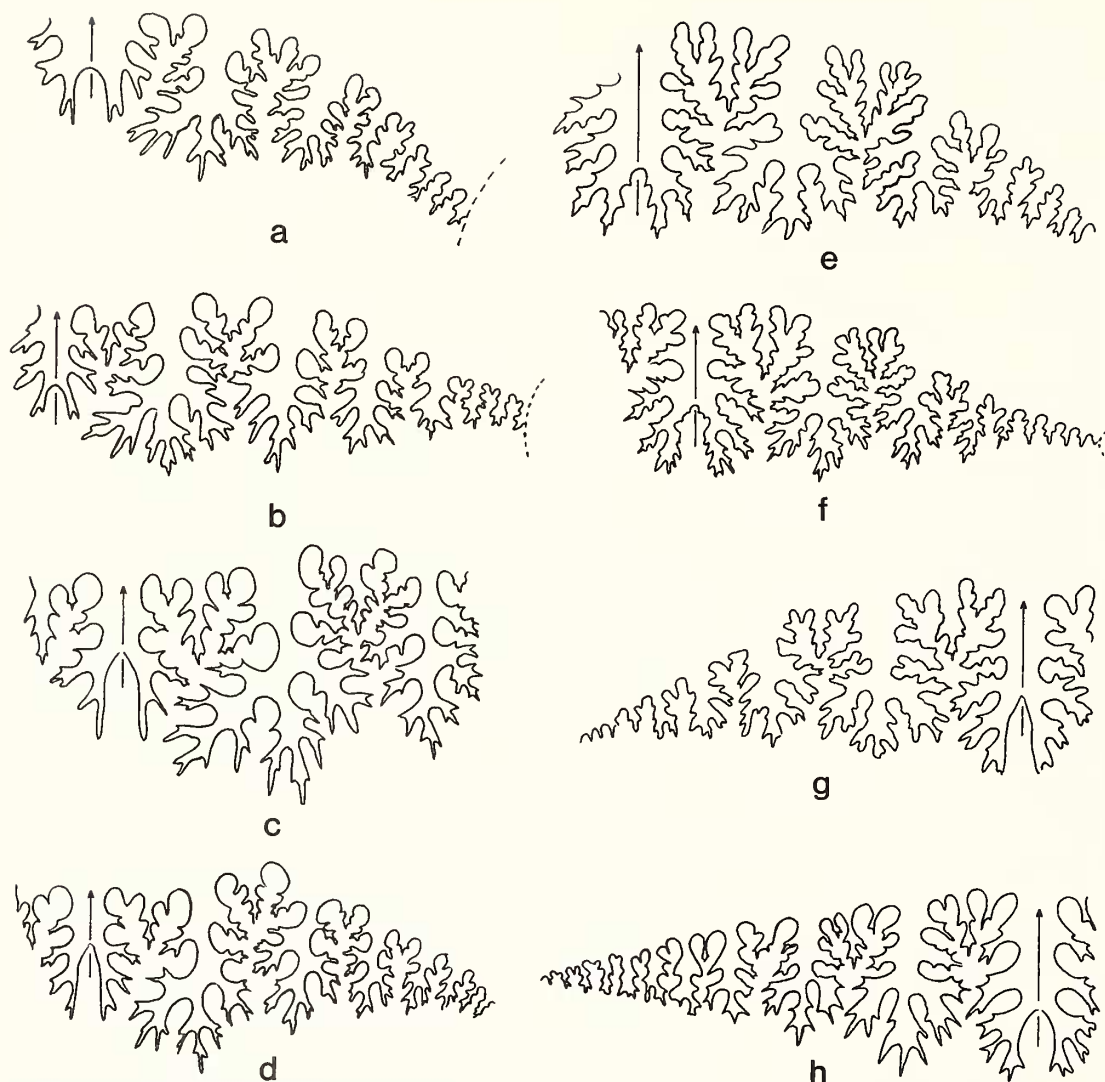
1846 *Ammonites rouyanus* d'Orbigny; Forbes, p. 108, pl. 8, fig. 6.

1850 *Ammonites forbesianum* d'Orbigny, p. 213.

1970 *Phyllopachyceras forbesianum* (d'Orbigny); Henderson, p. 7, pl. 1, figs. 2, 4, 5.

*Material.* Forty-nine specimens, localities 3, 4, 6, 8–12, 15–20, 22, and 25.

*Description.* Shell involute, expanding rapidly, the umbilicus measuring 3–4% of the shell diameter. Umbilical wall steep, sloping outwards, umbilical shoulder not clearly demarcated. Whorls equidimensional with well



TEXT-FIG. 3. Discrimination of *Partschiceras* (*Partschiceras*) and *Partschiceras* (*Phyllopachyceras*) by means of the external lobe of the suture. a-d, *Partschiceras* (*Partschiceras*). a, the type species of *Partschiceras* (*Partschiceras*), *P. (P.) partschi* (Stur), from Geyer 1893, pl. 5, fig. 9, middle Liassic,  $\times 6$ ; b, *P. (P.) reptroplicatum* (Geyer), from Geyer 1893, pl. 6, fig. 3c, middle Liassic,  $\times 3$ ; c, *P. (P.) subobtusum* (Kudernatsch), from Sturani 1966, pl. 5, fig. 3, lower Bathonian,  $\times 3$ ; d, *P. (P.) viator* (d'Orbigny), from Sturani 1966, pl. 5, fig. 1, upper Bathonian,  $\times 3$ . e-h, *Partschiceras* (*Phyllopachyceras*). e, *P. (P.) eichwaldi occidentale* Wiedmann, from Wiedmann 1964, text-fig. 55, Barremian,  $\times 3$ ; f, *P. (P.) forbesianum* (d'Orbigny), WAM 71.211b, lower Maastrichtian,  $\times 2.5$ ; g, the type species of *Partschiceras* (*Phyllopachyceras*), *P. (P.) infundibulum* (d'Orbigny), from Drushchits 1956, text-fig. 552,  $\times 3$ ; h, *P. (P.) rouyanum* (d'Orbigny), from d'Orbigny 1841, pl. 110, fig. 5, Neocomian,  $? \times 1\frac{1}{2}$ .

arched flanks and venter. Ornament of fine lirae, rursiradiate on the umbilical shoulder and rectiradiate on the flanks and venter for all growth stages. Broad, weak, rather closely spaced folds appear at a shell diameter of about 35 mm. Suture complex with small phylloid terminations on the major saddles; ten auxiliary saddles in the umbilical lobe arranged in a rectiradiate line.

*Dimensions.*

	D	H	B	B/H	U	%
Lectotype BM C51081	31.5	17.8	18.0	1.01	0.8	3
WAM 60.52b	35.0	18.0	18.0	1.00	1.25	4
WAM 80.835	41.0	24.0	23.5	0.98	1.25	3
WAM 71.2116	46.0	27.0	26.0	0.96	2.0	4
WAM 80.985	48.5	26.5	28.5	0.93	2.0	4
WAM 86.965	56.0	34.0	32.0	0.94	2.0	4

*Remarks.* *P. (P.) forbesianum* is a long-ranging species, first appearing in the lower Santonian of Madagascar (Collignon 1966) and extending into the lower Maastrichtian in Western Australia and India.

Suborder LYTOCERATINA Hyatt, 1899  
 Superfamily TETRAGONITACEAE Hyatt, 1900  
 Family GAUDRYCERATIDAE Spath, 1927  
 Genus ANAGAUDRYCERAS Shimizu, 1934

*Type species.* *Ammonites sacya* Forbes, 1846 (= *A. buddha* Forbes, 1846).

*Remarks.* The status and content of *Anagaudryceras* has recently been reviewed by Kennedy and Klinger (1979). It is a widely distributed genus with very conservative morphological trends. Individual species typically show marked ontogenetic change, juveniles tending to be widely umbilicate with depressed whorls ornamented with fine lirae. Adults are generally more narrowly umbilicate with less depressed or even compressed whorls and commonly bear broad weak ribs in addition to lirae. Most species are known from no more than a few specimens which are often insufficient to properly characterize ontogenetic changes and intraspecific variation. In consequence, there is a plethora of poorly characterized *Anagaudryceras* species in the literature, including the type species *Ammonites sacya* (Forbes) which has been considered synonymous with *A. buddha* (Forbes) by a number of authors. Contrary to the view of Kennedy and Klinger (1979), *A. sacya* is the senior synonym, having been designated as such by Stoliczka (1865).

*Anagaudryceras subtilineatum* (Kossmat, 1895)

Plate 2, figs. 3, 4; text-fig. 4a

1895 *Lytoceras* (*Gaudryceras*) *subtilineatum* Kossmat, p. 123, pl. 19 figs. 1a-c, ?2a, b.

1979 *Anagaudryceras subtilineatum* (Kossmat); Kennedy and Klinger, p. 155, pl. 14, figs. 3, 12; text-fig. 3.

*Material.* Three specimens, localities 4, 23, and 24.

*Description.* Early growth stages, up to a shell diameter of about 35 mm, have strongly depressed volutions (B/H ratio of about 1.6) with strongly convex flanks scarcely discriminated from the convex, outwardly sloping umbilical wall and broadly arched venter. Umbilical diameter is about half the shell diameter. Later growth stages, up to 45 mm, are a little less evolute and the whorls become much less depressed with less strongly convex flanks, a more clearly marked umbilical shoulder, and more narrowly arched venter. Ornament consists of very fine lirae and infrequent, weak constrictions each of which is preceded by a prominent collar. Constrictions are weakly prorsiradiate on the umbilical wall, swing more strongly forward on the dorsal flanks, straighten slightly on the ventral flanks, and swing forward again across the venter. As far as can be seen the lirae follow the same course. Suture typical of the genus with L bifid and U retracted on the umbilical wall and subdivided into numerous auxiliary elements. External saddle finely and evenly serrated.

*Dimensions.*

	D	H	B	B/H	U	%
WAM 83.2721	36.5	10.0	14.8	1.48	17.2	47
WAM 81.2347	24.0	6.8	11.0	1.62	12.2	51
WAM 81.2347	c. 45.5	15.2	18.8	1.23	20.5	c. 45

*Remarks.* The figured Western Australian specimen (Pl. 2, figs. 3, 4) matches, almost exactly, the larger of Kossmat's two specimens which Kennedy and Klinger (1979) designated as lectotype. Kossmat's smaller syntype has a somewhat less depressed whorl section (B/H ratio of 1.4 at a shell diameter of 15 mm) and its specific identity is questionable.

*Anagaudryceras politissimum* (Kossmat, 1895)

Plate 1, figs. 9-10; text-fig. 4d

1895 *Lytoceras* (*Gaudryceras*) *politissimum* Kossmat, p. 128, pl. 15, fig. 7a-c.

1979 *Anagaudryceras politissimum* (Kossmat); Kennedy and Klinger, p. 154, pl. 5, fig. 3.

*Material.* Nine specimens, localities 6, 12, 16, 17, 20, 22, and 23.

*Description.* Early growth stages, up to a shell diameter of 35-40 mm, have slightly depressed volutions and are evolute. Later growth stages become increasingly compressed and are slightly more narrowly umbilicate. Volutions subcircular in section with convex flanks which pass smoothly into an outward sloping, convex umbilical wall; venter broadly rounded. Ornament consists of dense, fine lirae and some four prominent collars per whorl, each followed by a weak constriction. These elements are parallel and follow a slightly sinuous course, being markedly prorsiradiate on the dorsal flanks and venter, but slightly less so on the umbilical wall and ventral flanks. Suture typical of the genus with a lanceolate external saddle, L bifid and U retracted on the umbilical wall, with numerous auxiliary elements.

*Dimensions.*

	D	H	B	B/H	U	%
WAM 83.2716	29.0	9.5	11.0	1.16	12.5	43
WAM 83.2714	47.5	17.5	16.5	0.94	19.2	40
WAM 83.2715	52.0	17.5	16.5	0.96	20.0	38
WAM 83.2720	114.0	47.0	42.5	0.90	42.0	36

*Remarks.* The largest Western Australian specimen is still septate at a shell diameter of 114 mm so that fully grown complete shells must have exceeded 150 mm in diameter. *A. politissimum* was a long-ranging (Turonian-Maastrichtian) inhabitant of the Indian Ocean.

Genus GAUDRYCERAS de Grossouvre, 1894

*Gaudryceras kayei* (Forbes, 1846)

Plate 1, figs. 13, 14; Plate 2, figs. 5, 6, 9, 10; text-fig. 4b, c

1846 *Ammonites kayei* Forbes, p. 101, pl. 8, fig. 3a, b.

1979 *Vertebrites kayei* (Forbes); Kennedy and Klinger, p. 160, pl. 14, fig. 2a-c; text-fig. 5.

*Material.* Twenty-two specimens, localities 5, 6, 12, 14-17, 20-22, and 25.

*Description.* Early whorls, to a shell diameter of some 50 mm, are depressed with a broad venter; they expand slowly and embrace only slightly so that the umbilicus exceeds 50% of the shell diameter. Later volutions are less depressed, becoming equidimensional at a shell diameter of some 75 mm, and have a more narrowly arched venter. They expand more rapidly and embrace more than the early volutions so that the umbilicus becomes narrower, representing 46% of the shell diameter on the largest measurable specimen available. Thin, sharp, wire-like lirae swing forward on the umbilical wall, straightening on the flanks where they split into very fine

EXPLANATION OF PLATE 2

Figs. 1-2. *Phylloceras* (*Neophylloceras*) *surya* (Forbes), WAM 60.50,  $\times 1$ .

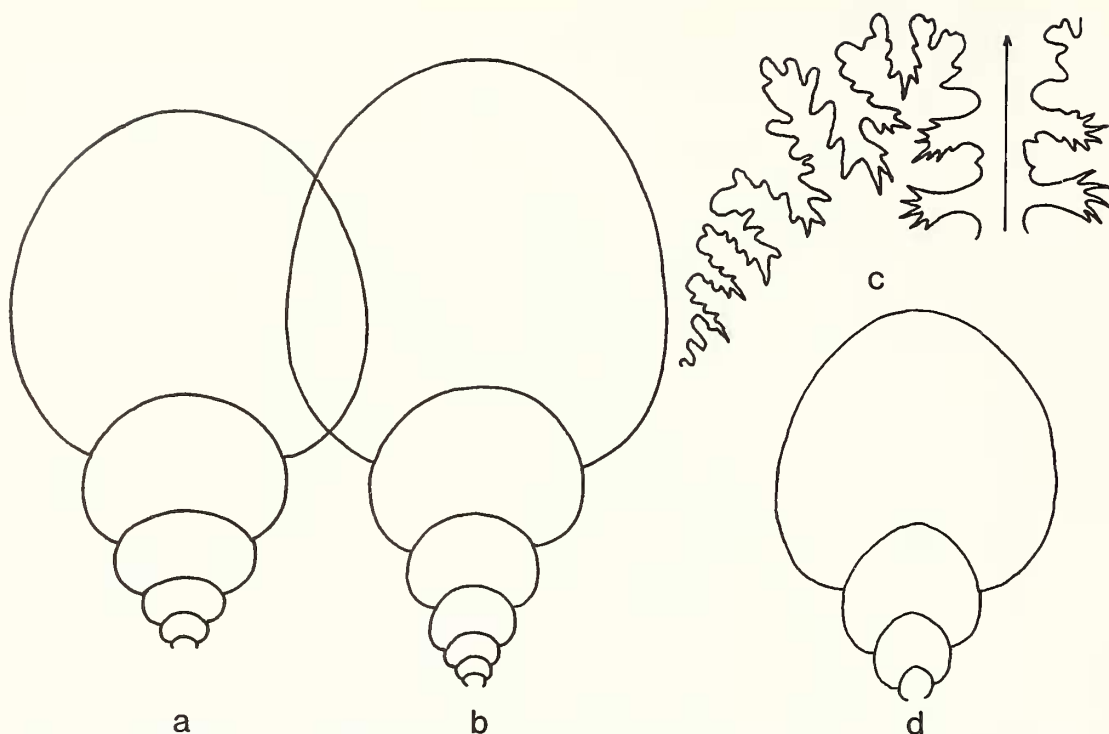
Figs. 3-4. *Anagaudryceras subtilineatum* (Kossmat), WAM 81.2347,  $\times 1$ .

Figs. 5-6, 9-10. *Gaudryceras kayei* (Forbes). 5-6, WAM 80.1002,  $\times 1$ . 9-10, WAM 80.977,  $\times 1$ .

Figs. 7-8. *Pseudophyllites indra* (Forbes), WAM 60.92d,  $\times 1$ .







TEXT-FIG. 4. *a*, whorl profile of *Anagaudryceras subtilineatum* (Kossmat), WAM 81.2347,  $\times 2$ . *b*, whorl profile of *Gaudryceras kayei* (Forbes), WAM 80.977,  $\times 2$ . *c*, internal suture of *G. kayei* (Forbes), WAM 80.839,  $\times 8$ . *d*, whorl profile of *A. politissimum* (Kossmat), WAM 81.2698,  $\times 2$ .

subdivisions which are weakly projected on the venter. Suture florid with the external saddle lanceolate, L bifid, and U deeply embayed with some fifteen auxiliary lobes.

#### Dimensions.

	D	H	B	B/H	U	%
WAM 80.1002	26.0	5.5	7.8	1.42	15.2	58
Lectotype: BM C51050	32.2	7.2	10.5	1.46	17.0	53
WAM 80.989	36.5	9.2	12.2	1.32	20.0	55
Syntype: BM C82498	36.5	9.2	12.0	1.30	18.2	50
WAM 82.3084	41.2	11.2	13.2	1.18	21.0	51
WAM 81.2611	55.0	17.0	19.0	1.12	26.5	47
Syntype: BM C51049	55.2	14.6	17.4	1.19	26.2	46
WAM 80.977	76.5	25.2	25.2	1.00	—	—
WAM 83.2701	—	47.0	44.8	0.95	—	—

*Remarks.* Ornamentation of the inner whorls, up to a shell diameter of 3 mm, shows on WAM 80.1002. Here the lirae are crowded together and the first whorl shows some fifteen regularly spaced stronger lirae, presumably marking constrictions. Later whorls have four to seven constrictions which are clear on internal moulds but faintly inscribed, or obscure, where the test is retained. Their primary lirae are separated by wide interspaces on the flanks, much wider than the lirae themselves.

*G. kayei* has been generally referred to *Vertebrites* Marshall, 1926, type species *V. murdocki* Marshall, having been included in that genus at its establishment. *V. murdocki* is characterized by a

serpenticone shell form with strongly depressed volutions persisting throughout all known ontogenetic stages to a shell diameter of 4.5 cm (Henderson 1970). It has conspicuous lirae on the flanks which split into very fine subdivisions at the margin of the venter. Arkell, Kummel and Wright (1957, fig. 230.3d) and Henderson (1970, text-fig. 5c) misrepresented the internal suture of *V. murdocki*, marking the umbilical seam as the internal lobe. Its suture (Marshall 1926, pl. 19, fig. 9; redrawn by Wiedmann 1962b, text-fig. 4i) is like that of *G. varicostatum* (Kennedy and Klinger 1979, text-fig. 1) and *Anagaudryceras particostatum* (Henderson 1970, text-fig. 5b).

The type series of *G. kayei*, now held by the British Museum (Natural History), contains only juvenile specimens, the largest of which is 55 mm in diameter. Larger specimens from Western Australia show that the juvenile serpenticone, with depressed volutions, strongly convex flanks, and a broadly arched venter, changes at a shell diameter of about 70 mm to a less widely umbilicate adult growth stage with equidimensional whorls showing gently convex flanks and a more narrowly arched venter. *G. kayei* is comparable with *G. varicostatum* van Hoepen (redescribed by Kennedy and Klinger 1979) except that the serpenticone shell form and fine ornament persist to a later stage of ontogeny. Separate generic status for *kaye*i is not warranted for such minor differences and it is regarded here as a member of *Gaudryceras*.

*V. murdocki* probably represents a *Gaudryceras* in which the paedomorphic tendencies of *G. kayei* are even more advanced. Larger specimens than currently available are needed to confirm its status and *Vertebrites* is perhaps best treated provisionally as a monotypic subgenus of *Gaudryceras*.

*Gaudryceras* sp.

*Material.* One specimen, WAM 83.3144, from locality 16.

*Description.* The specimen represents the last quarter whorl of a phragmocone which would have measured some 17 cm in diameter with an umbilical diameter of approximately 6 cm. Whorl profile compressed, with a whorl breadth/whorl height ratio of 0.75. Umbilical wall low and outwardly sloping, umbilical shoulder rounded, flanks weakly convex and slightly convergent, and venter well-rounded. Fine, dense ribs, some eighty per half whorl, begin from the umbilical seam. They are weakly prorsiradiate on the umbilical wall, shoulder, and dorsal flanks, straighten at the mid-flank, and swing slightly forward on the ventral flanks to be weakly projected across the venter. There is a single constriction with the same course as the ribs, preceded by a collar. Suture is deeply cut and highly dissected with L bifid.

*Remarks.* The specimen is a member of the *G. mite* species group of Kennedy and Klinger (1979) but more material is needed before its specific identity can be satisfactorily established. It may be compared with *G. beantalyense* Collignon (1956) but appears to differ in having less flexuous ribbing and lacking intercalatory ribs which appear on the dorsal flanks of the Madagascan species. It also resembles *G. vararaquense* Kossmat (1895) but is less finely ribbed.

Family TETRAGONITIDAE Hyatt, 1900  
Genus PSEUDOPHYLLITES Kossmat, 1895

*Type species.* *Ammonites indra* Forbes, 1846.

*Remarks.* Many of the species proposed for *Pseudophyllites* have passed into synonymy (Henderson 1970; Kennedy and Klinger 1977b) so that at present only three are regarded as valid. *P. indra* (Forbes) was widely distributed on the margins of north Pacific and Indian Oceans and ranged into Europe as far north as Poland and possibly as far west as south-eastern France. *P. latus* (Marshall) had a southern distribution (Antarctic Peninsula, southern Argentina, New Zealand, south-eastern Africa, Madagascar, and Western Australia) and was also represented in Greenland. Its disjunct distribution is reminiscent of the bipolar species distribution shown by planktonic Foraminifera (Bé 1977) and other microplankton. *P. teres* (van Hoepen) is known with certainty only from south-eastern Africa and Madagascar. *P. amphitrite* and *P. nereidideditus*, established by Maury (1930) for two Brazilian specimens, are of uncertain affinities. They may represent a separate local species or they may be junior synonyms as suggested by Kennedy and Klinger (1977b); more



material is needed to assess their status. The Austrian species *P. pastremus* (Redtenbacher 1873) is known only from poorly preserved material and is also a *nomen dubium*.

*Pseudophyllites latus* (Marshall, 1926)

Plate 3, figs. 1–3, 6–8; text-fig. 5b, c

1926 *Tetragonites latus* Marshall, p. 149, pl. 20, fig. 6, 6a; pl. 32, figs. 1, 2.

1965 *Pseudophyllites peregrinus* Spath; Hünicken, p. 53, pl. 1, figs. 5–7; pl. 7, figs. 3, 4.

1970 *Pseudophyllites latus* (Marshall); Henderson, p. 12, pl. 1, fig. 10a, b; pl. 2, fig. 3; text-fig. 4a, c.

1977b *Pseudophyllites latus* (Marshall); Kennedy and Klinger, p. 190, text-figs. 25, 26.

*Material.* Eight specimens, localities 6, 12, 16, 17, 19, and 23.

*Description.* Whorls equidimensional to slightly depressed, with a broadly arched venter. Umbilical wall vertical at the seam but curving outwards to merge with a broadly rounded umbilical shoulder. Umbilicus measures more than 20% of the shell diameter in early ontogeny, reducing to 19% at a shell diameter of 70 mm. Ornament is lacking. Septal recess and inner septum small for the genus; width of the latter is about 24% of the whorl diameter. External saddle of the suture is broad and spatulate; E is broad, L bifid, and U has its auxiliary elements arrayed in a rectilinear series.

*Dimensions.*

	D	H	B	B/H	U	%
WAM 81.2514	28.0	12.5	15.0	1.25	6.2	22
WAM 83.2692	40.0	20.5	20.5	1.00	7.8	20
WAM 83.2693	56.2	28.5	28.5	1.00	10.5	19
NMV P31019	70.0	35.0	36.0	1.02	13.0	19

*Remarks.* Morphological differences between *P. latus* and *P. indra* are subtle, involving slight changes in whorl proportions and shape, the size of the septal recess and inner septum, and the shape of the ventral saddle. This notwithstanding, morphology within each of the species is so consistent, even in disparate populations, that they are readily separable.

The range of *P. latus* is upper Santonian–lower Maastrichtian.

*Pseudophyllites indra* (Forbes, 1846)

Plate 2, figs. 7, 8; Plate 3, figs. 4, 5; text-fig. 5a, d

1846 *Ammonites indra* Forbes, p. 105, pl. 11, fig. 7a–c.

1977b *Pseudophyllites indra* (Forbes); Kennedy and Klinger, p. 182, text-figs. 19a–f, 20–22.

1980 *Pseudophyllites indra* (Forbes); Blaszkiewicz, p. 19, pl. 44, fig. 1.

*Material.* Seventy-two specimens, localities 3–7, 9–18, 20–23, and 25.

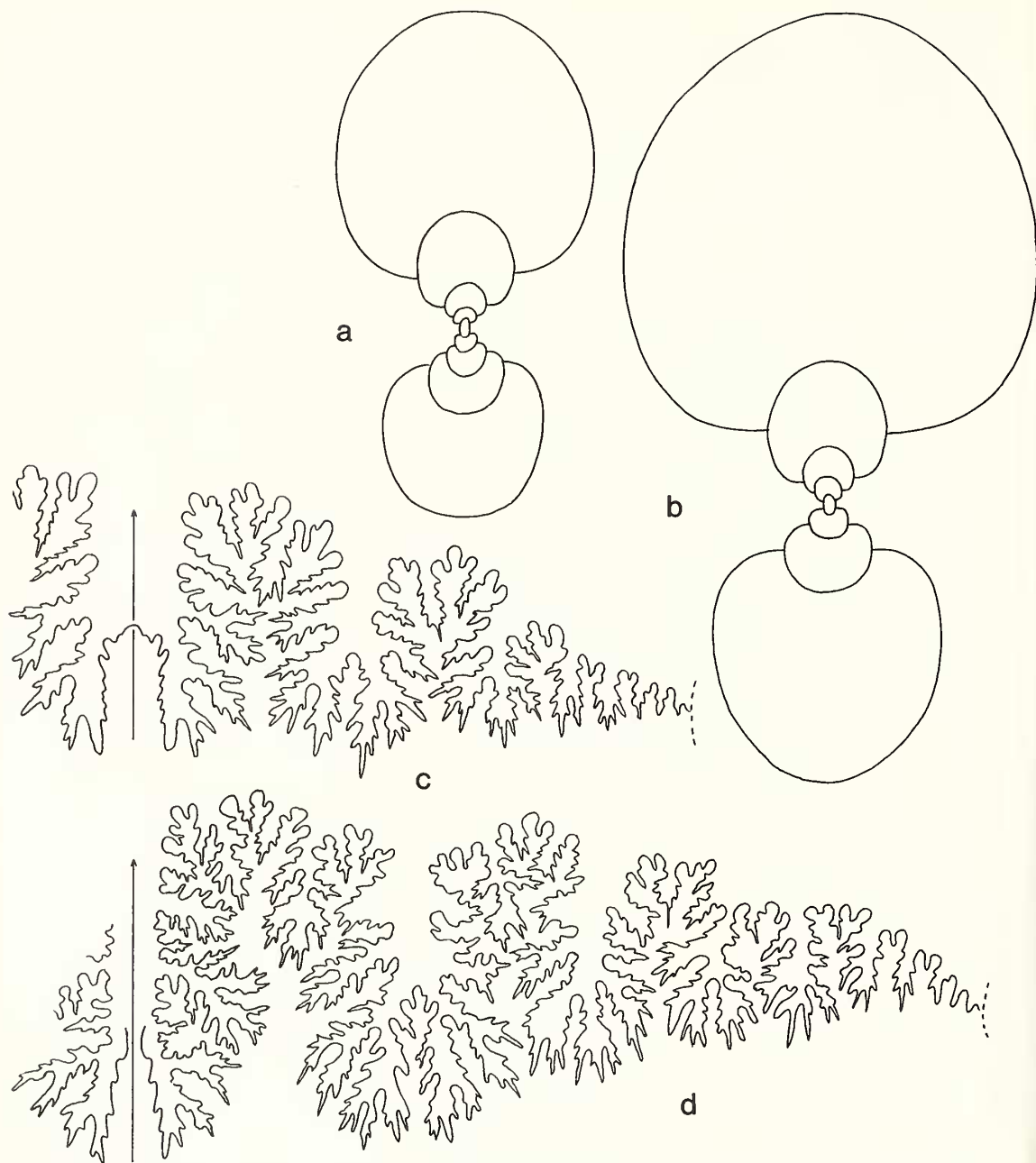
*Description.* Whorls very slightly compressed with a narrowly arched venter; umbilical wall curving gently outwards to a broadly rounded umbilical shoulder. Initial growth stages have an umbilicus measuring some 22% of the shell diameter, reducing to 16% at a shell diameter of 118 mm. Septal recess and inner septum large; width of the latter measures some 36% of the whorl width. Suture with a narrow lanceolate external saddle; E is narrow, L bifid, and U is slightly retracted on the umbilical wall.

EXPLANATION OF PLATE 3

Figs. 1–3, 6–8. *Pseudophyllites latus* (Marshall). 1–3, WAM 81.2514,  $\times 1$ . 6–8, NMV P31019,  $\times 1$ .  
Figs. 4–5. *P. indra* (Forbes), WAM 60.44a,  $\times 1$ .







TEXT-FIG. 5. Whorl profiles and sutures of *Pseudophyllites*. a, *P. indra* (Forbes), WAM 81.2433,  $\times 1.5$ . b, *P. latus* (Marshall), NMV P31019,  $\times 1.5$ . c, *P. latus* (Marshall), NMV P31019,  $\times 3$ . d, *P. indra* (Forbes), WAM 81.2433,  $\times 3$ .

*Dimensions.*

	D	H	B	B/H	U	%
WAM 81.2497	30.8	15.2	14.8	0.97	7.0	23
WAM 81.2358	43.0	21.5	20.8	0.97	9.0	21
WAM 60.92d	52.0	27.5	27.0	0.98	10.5	20
WAM 10571	70.0	35.8	33.5	0.94	13.0	19
WAM 80.972	80.5	41.5	39.0	0.94	15.2	19
WAM 81.2609a	91.0	47.5	46.2	0.97	16.8	18
Lectotype: BM C51068	110.0	58.0	54.0	0.93	18.0	16
WAM 60.44a	110.0	58.5	56.0	0.96	20.0	18
WAM 60.44b	116.0	66.0	58.0	0.97	22.0	19
WAM 81.2500	172.0	98.0	96.0	0.98	27.5	16

*Remarks.* The Western Australian suite matches exactly with Forbes's original type series comprised of more than twenty-five specimens and held by the British Museum (Natural History). It displays the complex lytoceratid septal surface in exceptional detail, as described elsewhere (Henderson 1984).

Specimens retaining the shell show that weak ribs appear on the flanks at a shell diameter of about 40 mm. The largest specimen is still separate at a shell diameter of 17.2 cm, indicating that adult members of the species must have reached diameters of 25 cm or more.

*P. indra* has an established range of early Campanian–Maastrichtian. In south-eastern Africa its range may perhaps extend down into the later Santonian (Kennedy and Klinger 1977b).

Suborder AMMONITINA Hyatt, 1889  
 Superfamily DESMOCERATACEAE Zittel, 1895  
 Family DESMOCERATIDAE Zittel, 1895  
 Subfamily DESMOCERATINAE Zittel, 1895  
 Genus DESMOPHYLLITES Spath, 1929

1894 *Schluteria* de Grossouvre (*non* Fritsch 1887), p. 216.

1938 *Schlutericeras* Collignon (*non* Hyatt 1903), p. 92.

*Type species:* *Desmoceras larteti* Seunes, 1891.

*Remarks.* *Desmophyllites* is little different from *Desmoceras* (*Pseudouhligella*) Matsumoto, 1942a, being distinguished only by its more embracing volution and narrower umbilicus, the wall of which has its upper portion sloping outwards and passing into the umbilical shoulder in a smooth curve. In *Desmoceras* (*Pseudouhligella*) the umbilical wall is vertical and the shoulder abrupt. The internal suture of *Desmoceras* (*Pseudouhligella*) has not as yet been described but it probably has fewer auxiliary divisions of the umbilical lobe than that of *Desmophyllites*.

As noted by Matsumoto (1954a), the ranges of these two taxa are disjunct, *Desmophyllites* ranging no lower than Santonian and *Desmoceras* (*Pseudouhligella*) ranging no higher than Cenomanian. It may be that *Damesites* Matsumoto, 1942a was the progenitor of *Desmophyllites*. It is well known from Turonian and Coniacian strata and differs from *Desmophyllites* only in possessing a keel. Body chambers of *D. diphyloides* with a weak mid-ventral ridge described by Matsumoto (1959b) from California offer some support to this proposal.

Only two named species of *Desmophyllites* are recognized here: *D. larteti* (Seunes) characterized by compressed whorls with a B/H ratio of 0.5–0.6 at a shell diameter of some 8 cm and *D. diphyloides* (Forbes) which is less compressed, its whorls having a B/H ratio of 0.7–0.8 at a comparable shell size. Only two specimens of *D. larteti*, both from Maastrichtian chalk facies in France, have been described. It is possible that they represent *D. diphyloides* flattened by compression and they need re-evaluation. The fragmentary specimen described from the Antarctic Peninsula by Howarth (1958) is more widely umbilicate than either *D. diphyloides* or *D. larteti* and appears to represent an undescribed species.

*Desmophyllites diphylloides* (Forbes, 1846)

## Plate 4, figs. 1-4

- 1846 *Ammonites diphylloides* Forbes, p. 105, pl. 8, fig. 8a-c.  
 1894 *Desmoceras pyrenaicum* de Grossouvre (*pars*), p. 168, pl. 37, fig. 9a-c (*non* pl. 25, fig. 2a, b).  
 1898 *Desmoceras phyllimorphum* Kossmat, p. 110, pl. 19, fig. 10a-c.  
 1921 *Schluteria woodsi* Spath, p. 45, fig. 1.  
 1938 *Schluteria larteti* (Seunes); Collignon, p. 42, pl. 7, fig. 3, 3a, text-figs. K, L.  
 1959b *Desmophyllites diphylloides* (Forbes); Matsumoto, p. 9, pl. 3, fig. 3a-c, text-fig. 2.  
 1931 *Desmophyllites diphylloides* var. *besairiei* Collignon, p. 15, pl. 2, fig. 8, 8a, b; pl. 8, figs. 5-8.  
 1961 *Desmophyllites diphylloides* var. *inermis* Collignon, p. 63, pl. 24, figs. 4, 4a, 4b, 5, 5a, 5b; pl. 25, fig. 3, 3a, 3b.  
 1961 *Desmophyllites diphylloides* var. *lata* Collignon, p. 64, pl. 25, figs. 7, 7a, 7b, 8, 8a, 8b, text-fig. 4.  
 1961 *Desmophyllites phyllimorphus* (Kossmat); Collignon, p. 65, pl. 26, fig. 1, 1a, b, text-fig. 5.  
 1961 *Desmophyllites larteti* (Seunes); Collignon, p. 66, pl. 26, fig. 2, 2a, b, text-fig. 6.  
 1963 *Desmophyllites phyllimorphus* (Kossmat); Jones, p. 34, pl. 10, figs. 4-6.  
 1965 *Desmophyllites diphylloides* (Forbes); Howarth, p. 388, pl. 11, fig. 3a, b.  
 1980 *Desmophyllites diphylloides* (Forbes); Blasco *et al.*, p. 483, pl. 2, figs. 9-15.

*Material.* Thirty-two specimens, localities 4-9, 11, 12, 15-18, 20, 23, and 25.

*Description.* Umbilicus a steep-walled pit measuring 7-9% of the shell diameter. Whorls embracing with very weakly convex, subparallel flanks and a broadly arched venter; they are compressed with the whorl breadth/whorl height ratio reducing from about 0.87 at a shell diameter of 20-25 mm to about 0.76 at a shell diameter of 75 mm. Axis of maximum whorl width is slightly ventral of the mid-flanks. Shell smooth apart from shallowly impressed constrictions which are weakly flexuous on the flanks and quite strongly projected on the venter. Suture with finely divided elements. E almost as deep as L which is trifid, U has some fifteen auxiliary saddles, and I is bifid.

*Dimensions.*

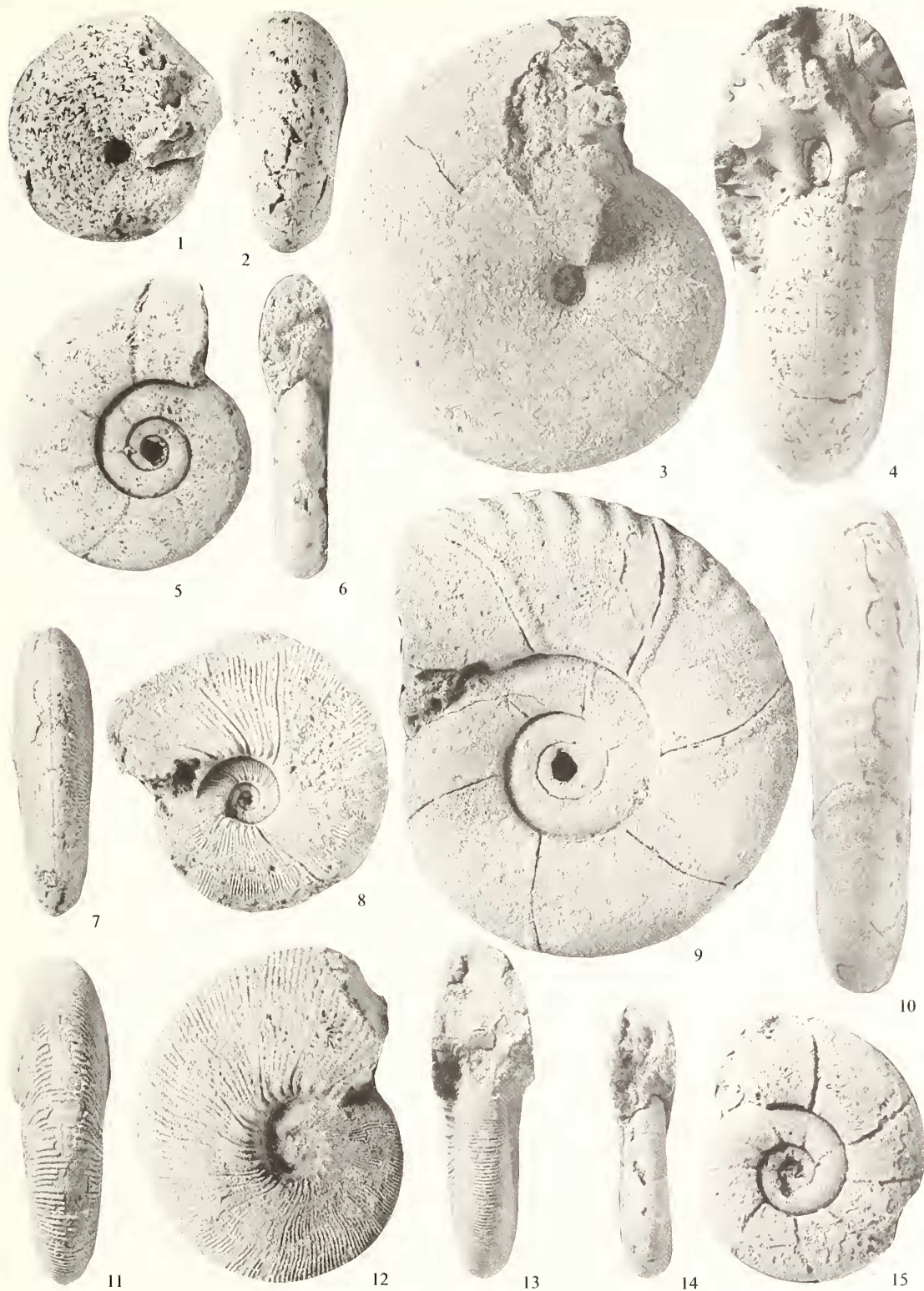
	D	B	H	B/H	U	%
Lectotype: BM C22682	20.2	10.8	9.2	0.85	1.2	5
WAM 80.837	24.5	12.5	10.8	0.86	1.5	6
WAM 81.2618	35.0	18.0	15.5	0.86	2.0	6
WAM 71.212	40.5	20.5	17.2	0.86	3.2	8
WAM 81.2680	46.0	24.5	19.2	0.78	4.0	9
WAM 60.92a	51.0	26.0	21.5	0.83	4.5	9
WAM 81.2520	61.0	32.0	26.2	0.82	5.2	8
WAM 81.2694	70.0	37.0	29.2	0.77	5.8	8
WAM 60.52a	75.0	40.0	32.8	0.82	6.0	8
WAM 81.2600	77.0	41.0	31.2	0.76	6.0	8

*Remarks.* Forbes's type series from Pondicherry, India, now held by the British Museum (Natural History), are all juvenile specimens and the lack of adults has in the past resulted in uncertainty in the definition of the species. The Western Australian suite allows documentation of the shell ontogeny to a diameter of nearly 8 cm. Whorls become more slender with growth. They all show weakly convex flanks but among the specimens, especially juveniles, the convexity is slightly variable. The number and shape of constrictions is also variable. They show clearly only on internal moulds and are more

## EXPLANATION OF PLATE 4

- Figs. 1-4. *Desmophyllites diphylloides* (Forbes). 1-2, WAM 81.2449,  $\times 1$ . 3-4, WAM 81.2694,  $\times 1$ .  
 Figs. 5-6, 9-10, 14-15. *Kitchinites spathi* sp. nov. 5-6, paratype, WAM 71.209a,  $\times 1$ . 9-10, holotype, WAM 84.632,  $\times 1$ . 14-15, paratype, WAM 71.209b,  $\times 1$ .  
 Figs. 7-8, 11-13. *Maorites densicostatus* (Kilian and Reboul). 7-8, WAM 80.847,  $\times 1$ . 11-13, WAM 80.1000,  $\times 1$ .





typical of juveniles which have as many as eight per whorl rather than adult whorls which may show as few as two. On some shells they are quite flexuous on the flanks whereas on others they are almost straight. The umbilical wall is convex, overhanging near the umbilical seam, and turned outwards near the umbilical shoulder. Measurements of the umbilicus given here represent minimum diameters; measurements in the literature suggesting a wider umbilicus for *D. diphylloides* were doubtless taken at the base of the umbilical shoulder.

The ontogenetic change in whorl shape and variation in constrictions shown by the Western Australian specimens necessitate a wider definition of *D. diphylloides* than that adopted by most previous commentators. The large, slender whorled specimen from Trichonopoly, India, on which Kossmat (1898) based *D. phyllimorphum*, is best regarded as an adult *D. diphylloides*. It has a whorl breadth/whorl height ratio of 0.70 at a shell diameter 81.5 mm and is only slightly more compressed than Western Australian specimens of equivalent size. The large Alaskan specimens recorded by Jones (1963) as *D. phyllimorphum* because of their slender whorls are likewise adult *D. diphylloides*. Juvenile *Desmophyllites* from the Pacific coast of North America, originally described by Whiteaves (1879), Usher (1952), and Anderson (1958) as local species, were united with *D. diphylloides* by Matsumoto (1959b).

Slight changes in whorl shape and the nature of constrictions, used by Collignon (1931, 1938, 1961, 1966, 1971) to discriminate no less than three species and four varieties of *Desmophyllites* from Madagascar, are treated here as representing intraspecific variation within a single species of which *D. diphylloides* is the senior synonym. New species erected by van Hoepen (1921) and Spath (1921) from south-eastern Africa are also regarded as falling within the compass of *D. diphylloides* (see Matsumoto 1959b), as is the specimen figured by de Grossouvre (1894, pl. 37, fig. 9a-c) as *Desmoceras pyrenaicum* but unrelated to the primary type of that species (de Grossouvre 1894, pl. 25, fig. 2a, b).

*Desmophyllites diphylloides* was widely distributed on the margins of the Indian and Pacific Oceans and spread westward along the Tethyan seaway to reach North Africa and southern France. It has an established range of lower Santonian–Maastrichtian.

#### Subfamily PUZOSIINAE Spath, 1922

##### Genus KITCHINITES Spath, 1922

1922 *Kitchinites* Spath, p. 127.

1954b *Neopuzosia* Matsumoto, p. 89.

?1953 *Oiophyllites* Spath, p. 21.

*Type species. Holcodiscus pondicherryanus* Kossmat, 1897a.

*Remarks.* *Neopuzosia*, with type species *N. japonicus* (Spath), was introduced by Matsumoto (1954b) to separate Japanese Santonian–lower Campanian species from Campanian–Maastrichtian *Kitchinites* (s.s.). Howarth (1965), however, convincingly argued that these two taxa are better treated as synonyms, rather than as subgenera of *Kitchinites* (s.l.) as has been common practice.

*Oiophyllites* Spath (1953) was based on *O. decipiens* Spath known only from juvenile specimens from the Antarctic Peninsula, the largest of which measures 20 mm in diameter. A second species, *O. angolaensis* Spath (1953), was based on a single juvenile specimen from Angola, 21 mm in diameter. *Oiophyllites* differs from *Kitchinites* principally in having a smooth shell. However, in some species of *Kitchinites*, such as *K. darwini* (Steinmann) (redescribed by Howarth 1966), the juvenile shell is smooth to a diameter of 30 mm. It therefore seems likely that both *Oiophyllites* species are merely juvenile *Kitchinites*. It is noteworthy that *Oiophyllites* and large *Kitchinites* are known from the same locality in Angola (Howarth 1965) and occur at separate but broadly coeval localities in the Antarctic Peninsula (Howarth 1966).

*Kitchinites* is little different from its presumed ancestor *Mesopuzosia* Matsumoto (1954b), based on the Turonian–Coniacian species *M. pacifica* Matsumoto. The whorl profile of *Mesopuzosia*, which is rounded rather than compressed, allows its separation.

Sixteen nominate species of *Kitchinites* (= *Neopusozia*) have been proposed in all if the Western Australian species described here is included. Six were described from Madagascar by Collignon (1961) but all are round-whorled taxa and better transferred to *Mesopusozia*. The remainder are distributed on the borderlands of the Indo-West Pacific and South Atlantic Oceans, having been recorded from Saghalien, Hokkaido, New Zealand, Western Australia, India, Angola, the Antarctic Peninsula, and southern South America. They range in age from Santonian to Maastrichtian.

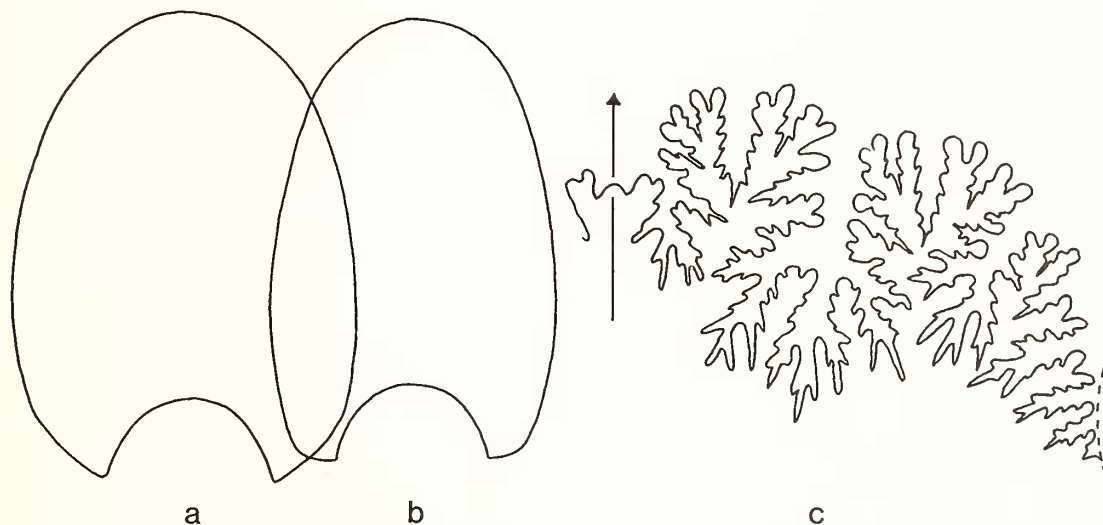
*Kitchinites spathi* sp. nov.

Plate 4, figs. 5, 6, 9, 10, 14, 15; text-fig. 6b, c

1941 *Hauericeras* sp. Spath, p. 43.

1941 *Kitchinites* sp. Spath, p. 45.

**Material.** Holotype WAM 84.632, locality 8. Paratypes WAM 81.2410, locality 4; WAM 81.2703, locality 6; WAM 71.209a, 71.209b, locality 8; NMV P31022, locality 11; WAM 80.971, 80.995, locality 12; WAM 81.2630, locality 15; WAM 10572, locality 16. Thirty-five additional specimens, localities 3–5, 7, 9, 10, 12, 16–18, 20, and 23–25.



TEXT-FIG. 6. a, whorl profile of *Neograhamites carnarvonensis* sp. nov., holotype, WAM 80.840,  $\times 4$ . b, whorl profile of *Kitchinites spathi* sp. nov., paratype, WAM 80.971,  $\times 2$ . c, suture of *K. spathi* sp. nov., paratype, WAM 71.209a,  $\times 4$ .

**Description.** Shell evolute and discoidal with whorl breadth/whorl height 0.63–0.76 and the umbilicus measuring 37–42% of the shell diameter. Umbilical wall low, subvertical, and sharply reflected at the umbilical shoulder which is narrowly rounded. Flanks subparallel and very weakly convex; venter smoothly rounded. Early whorls have no ribs apart from growth lines, but broad, rounded costae, numbering about twenty per half whorl and confined to the ventral flanks and venter, appear at a shell diameter of 60 mm. Initially costae are prorsiradial but they bend forward at the margin of the venter across which they are gently projected. Narrow constrictions, each preceded by a prominent collar, number three to six per half whorl beginning at a shell diameter of less than 1 cm. They are prorsiradial and almost straight across the umbilical wall and flanks and are strongly projected across the venter where they commonly truncate one rib. Suture with finely divided minor elements for the genus and a strongly retracted suspensory lobe.



*Dimensions.*

	D	H	B	B/H	U	%
WAM 81.2703	27.0	9.5	7.0	0.73	10.8	40
WAM 81.2630	36.5	11.8	9.0	0.76	14.8	41
NMV P31022	40.0	14.5	10.5	0.72	15.0	37
WAM 80.995	42.0	15.5	10.0	0.64	15.8	38
WAM 71.209a	47.0	11.0	15.5	0.71	19.0	40
NMV P31015	52.0	17.0	11.0	0.65	22.0	42
NMV P31013	76.0	26.0	17.8	0.68	30.5	40
WAM 10572	84.5	29.8	19.2	0.64	33.5	40

*Remarks.* Whorl dimensions are somewhat variable between different specimens but whorl breadth/whorl height ratio tends to reduce as ontogeny proceeds. The most mature whorl fragment in the collection shows that the strong costation persists to a shell diameter of some 105 mm at least.

The suite of specimens now available shows that the juvenile and adult whorl fragments described by Spath (1941) as *Hauericeras* sp. and *Kitchinites* sp. respectively are conspecific.

*K. spathi* is related to *K. darwini* (Steinmann) (redescribed by Howarth 1966), *K. angusta* (Marshall) (redescribed by Henderson 1970), and *K. angolaensis* Howarth 1965, in which the ribs are restricted to the ventral flanks and venter for at least part of the ontogeny. In *darwini* and *angolaensis* the ribs are more subdued and more closely spaced than in *spathi*. *K. angusta* is distinguished from *spathi* in being more narrowly umbilicate and having thinner costae which are more strongly projected across the venter.

Family KOSSMATICERATIDAE Spath, 1922  
Subfamily KOSSMATICERATINAE Spath, 1922  
Genus GUNNARITES Kilian and Reboul, 1909

1909 *Gunnarites* Kilian and Reboul, p. 26.

*Type species.* *G. antarcticus* (Weller, 1903, p. 417, pl. 11, figs. 1, 2).

*Remarks.* Western Australian *Gunnarites* are allied to taxa from the Antarctic Peninsula. Species determination, however, has been poorly documented for the Antarctic suite and subject to widely differing views. Kilian and Reboul (1909), in establishing the genus, recognized *G. antarcticus* (Weller) and *G. kalika* (Stoliczka) as well as three varieties to express variation in *G. antarcticus*. A third species, *G. gunnari*, they mistakenly referred to *Kossmaticeras*. Spath (1953) raised one of Kilian and Reboul's *antarcticus* varieties, var. *bhavaniformis*, to species rank and introduced four new species to make a total of eight. In addition, Spath introduced a plethora of varieties to cover specimens of intermediate morphology.

Howarth (1966) rationalized the suite to five species, three of which display appreciable intraspecific variation: *G. kalika* Stoliczka (= *Maorites pseudobhavanii* Spath), *G. antarcticus* Weller (= *G. paucinodatus* Spath, *G. rotundus* Spath, and *G. flexuosus* var. *transitoria* Spath), *G. bhavaniformis* Kilian and Reboul (= *G. flexuosus* Spath), *G. gunnari* (Kilian and Reboul), and *G. pachys* Spath.

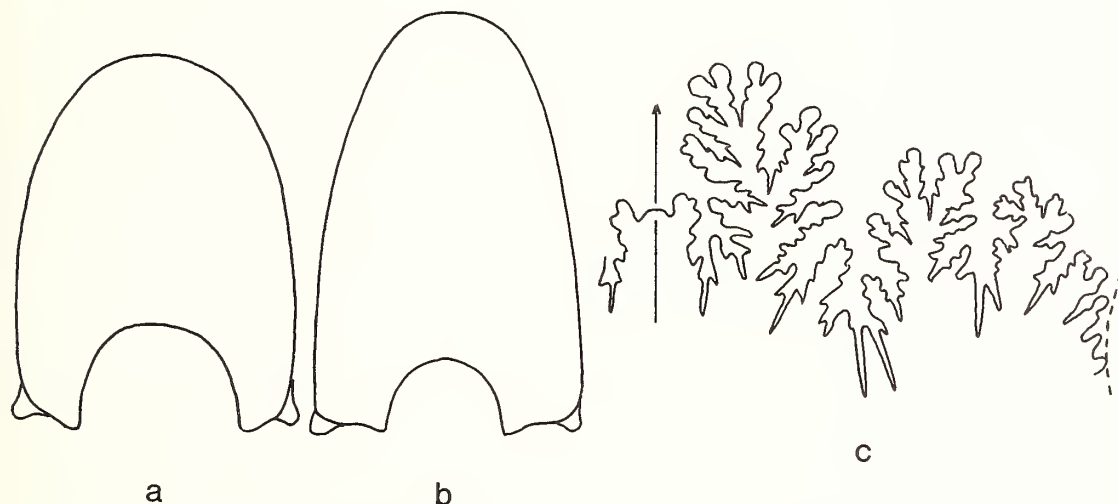
One of us (R.A.H.) has re-examined the Antarctic Peninsula collections on which Spath worked, held by the British Museum (Natural History), and generally endorses Howarth's (1966) synonymies. Shell measurements and rib counts, however, show that the range of variation between Antarctic specimens referred to *kalika* and *bhavaniformis* is continuous (text-fig. 8). They are treated here as a single variable species under the name *bhavaniformis*, and considered distinct from *G. kalika* Stoliczka. The status of *G. rotundus* is questionable. The type series consists of internal moulds but one specimen, BM C41370, retains fragments of shell showing that the ribs are not crenulate on the venter up to a shell diameter of 35 mm. This species is more likely to represent *Kossmaticeras* (*Natalites*) than *Gunnarites*.

*Gunnarites kalika* (Stoliczka, 1865)

Plate 5, figs. 8–15; text-figs. 7b, c, 8

- 1865 *Anmonites kalika* Stoliczka, p. 140, pl. 70, fig. 5a, b.  
 non 1909 *Gunnarites kalika* Stoliczka; Kilian and Reboul, p. 34.  
 1936 *Gunnarites* [sic] *kalika* Stoliczka; Whitehouse in Raggatt, p. 160.  
 1941 *Kosmaticeras* sp. nov.? aff. *aemilianus* Stoliczka; Spath, p. 44, pl. 1, fig. 2a, b.  
 non 1953 *Gunnarites kalika* Stoliczka; Spath, p. 33, pl. 10, figs. 1–6.  
 non 1966 *Gunnarites kalika* Stoliczka; Howarth, p. 67.  
 1980 *Gunnarites* sp. cf. *kalika* Stoliczka; Klinger *et al.*, p. 299, text-figs. 6A, B.  
 non 1980 *Gunnarites kalika* Stoliczka; Blasco *et al.*, p. 487, pl. 4, figs. 2–4.

*Material.* One hundred and sixty-one specimens, localities, 1, 3–20, and 22–25.



TEXT-FIG. 7. a, whorl profile of *Gunnarites bhavaniformis* (Kilian and Reboul), BM C41333,  $\times 2$ . b, whorl profile of *G. kalika* (Stoliczka), NMV P31026,  $\times 2$ . c, Suture of *G. kalika* (Stoliczka), WAM 81.2404,  $\times 4$ .

*Description.* Shell discoidal with whorl breadth/whorl height ratio of 0.6–0.76, and involute with the umbilical diameter 21–26% of the shell diameter. Umbilical wall vertical, or overhanging where it is produced into umbilical bullae; flanks weakly convex, converging towards the venter which is narrowly rounded. Twenty to twenty-five bullae per whorl mark the umbilical shoulder, each typically with a slight rursiradiate inclination. Segments of the umbilical shoulder are straight on many specimens giving the umbilicus a polygonal appearance. Ribs are slender and closely spaced, prorsiradiate and slightly flexuous. They number forty-one to seventy-two per half whorl, springing in bundles of three to five from the umbilical bullae with occasional intercalatories appearing in the mid-flank region. On the flanks they display smooth crests but are finely crenulate across the venter. Six to eleven somewhat flexuous constrictions per whorl, narrow on surfaces retaining shell and broader on internal moulds. Each is bordered by ridges, that on the adapical side typically being the strongest. Constrictions are more strongly prorsiradiate than the ribs so that three to five of the latter are truncated. Suture florid and deeply incised with lobe terminations overprinting the saddle extremities of the previous suture; E is broad and shallower than L and it is strongly retracted on the umbilical wall.

*Dimensions.* See text-fig. 8.

*Remarks.* The abundant material allows documentation of intraspecific variation. Shell shape is relatively constant across the suite but the density of ribbing shows very wide variation between

individual specimens (text-fig. 8). The largest specimen (WAM 81.2636; pl. 5, fig. 15) has part of the body chamber preserved and perhaps shows a mature ornament. Some of the ribs on the last segment of preserved whorl become feeble. The number of ribs on the last half-whorl (forty-one) and the number of constrictions (seven) represent the extreme limit of variation whereas the inner whorls are more densely ribbed and carry few constrictions. The south-eastern African specimen of *G. kalika* described by Kennedy and Klinger (in press) likewise has sparse ribbing on the last half whorl compared with earlier volutions and the last segment of preserved whorl is marked by feeble ribbing. Crenulation of the ribs has not been confirmed for shell diameters less than 3 cm and juvenile shells might easily be confused with *Maorites*.

The identity of these West Australian specimens with *G. kalika*, which was described from a single south Indian specimen, is clear from their shell dimensions and ornament (text-fig. 8). Spath (1941) mistakenly referred the species to *Kossmaticeras*, doubtless because the specimens at his disposal were internal moulds and did not show the distinctive rib crenulation.

The Antarctic Peninsula *G. kalika* of Kilian and Reboul (1909) and Spath (1953) (= *M. pseudobhavani* Spath, see Howarth 1966, p. 67) are here considered to be conspecific with *G. bhavaniformis* Kilian and Reboul. The range of variation in shell characteristics is continuous between specimens referred to these two species by Spath and consistently different from the population of Western Australia *G. kalika* to which Stoliczka's type specimen clearly belongs (text-fig. 8). The name *bhavaniformis* is retained for the Antarctic species. The Patagonian specimen referred to *G. kalika* by Blasco *et al.* (1980) develops very coarse ribbing at a shell diameter less than 50 mm after a finely ribbed initial stage of growth. It appears to be unrelated to either *G. bhavaniformis* Kilian and Reboul, or *G. kalika*, as redefined here.

*G. kalika* is known from the early Maastrichtian of south-eastern Africa (Klinger *et al.*, 1980; Kennedy and Klinger in press) and of Western Australia. The Indian type specimen is from the Ariyalur stage and is probably also of Maastrichtian age.

*Gunnarites raggatti* sp. nov.

Plate 6, figs. 1-4, 9, 10

?1980 *Gunnarites kalika* Stoliczka; Blasco *et al.*, p. 487, pl. 4, figs. 2-4.

*Material.* Holotype WAM 81.2542, locality 5. Paratypes UWA 97367, locality 1; WAM 81.2513, locality 5; WAM 81.2645, locality 6; WAM 83.2708, locality 25.

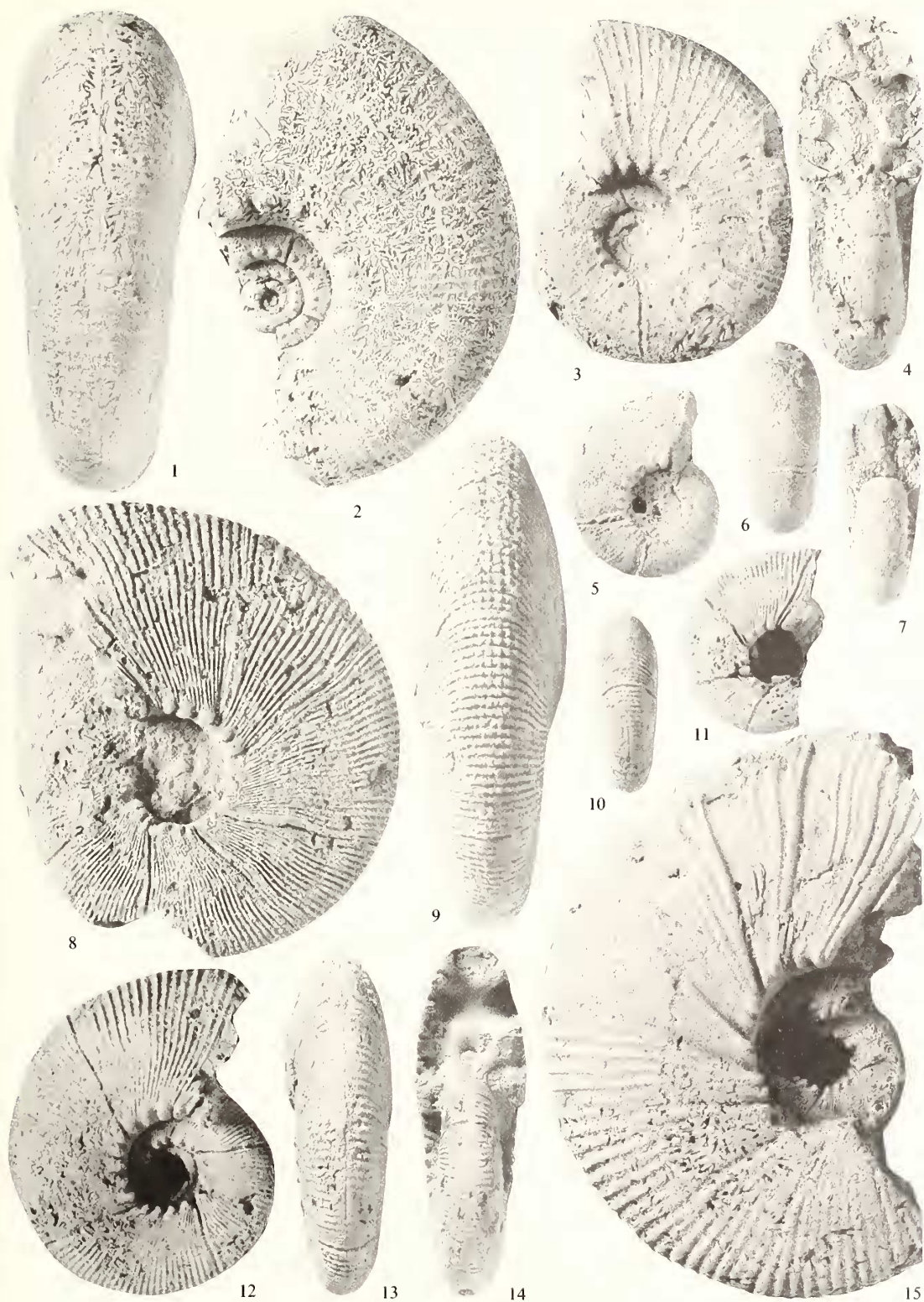
*Description.* Juvenile growth stages, up to a shell diameter of 40 mm, have an almost equidimensional whorl profile and are evolute with the umbilical diameter measuring 36 % of the shell diameter. During later growth, the whorl section becomes compressed and the coiling slightly more involute, the umbilical diameter reducing to 33 % of the shell diameter. Umbilical wall subvertical, umbilical shoulder abrupt, flanks flattened and slightly convergent, and venter broadly rounded. Ribs are thin and sharp, separated by broad interspaces and finely crenulate on the venter and ventral flanks. They swing gently forward from the umbilical shoulder and straighten in the mid-flank region to be retriradiate across the venter. On juvenile whorls, up to a shell diameter of 40 mm, they number seventy-five to eighty per whorl, springing in bundles of three and four from ten to eleven umbilical bullae with as many as five additional ribs arising from the umbilical shoulder between bullae.

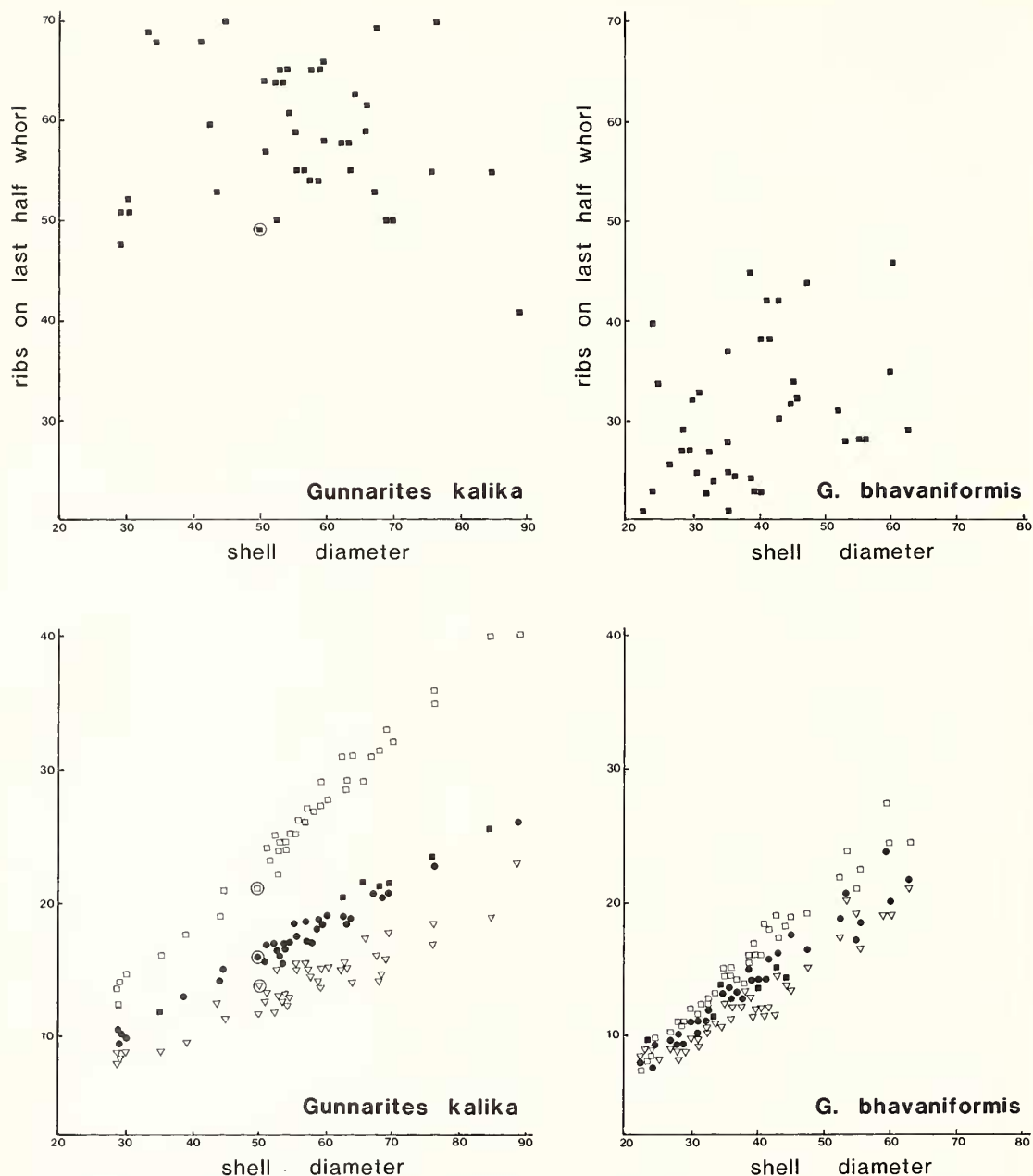
EXPLANATION OF PLATE 5

Figs. 1-7. *Grossouvrites gemmatus* (Huppé). 1-2, WAM 80.842,  $\times 1$ . 2-3, WAM 81.2521,  $\times 1$ . 5-7, WAM 81.2634,  $\times 1$ .

Figs. 8-15. *Gunnarites kalika* (Stoliczka). 8-9, NMV P31012,  $\times 1$ . 10-11, WAM 81.2496,  $\times 1$ . 12-14, NMV P31026,  $\times 1$ . 15, WAM 81.2636,  $\times 1$ .







TEXT-FIG. 8. Ribbing densities (upper) and shell measurements (lower) for *Gunnarites kalika* (Stoliczka) and *G. bhavaniformis* (Kilian and Reboul) inclusive of *G. kalika* Spath *non* Stoliczka. In the shell measurement plots squares represent whorl height, dots represent whorl breadth, and triangles represent umbilical width. Points representing the type specimen of *G. kalika* based on Stoliczka 1865, pl. 70, fig. 5a, b, are shown by symbols enclosed in a circle. Scales are in millimetres.

Constrictions number four to eight per whorl, becoming more numerous as the shell diameter increases; they are straight and prorsiradiate, each truncating one or two ribs. Suture, with E shallow, L deep and asymmetrically trifold, and U retracted on the umbilical wall, is typical of the genus.

*Dimensions.*

	D	H	B	B/H	U	%
WAM 81.2645	36.0	12.8	12.5	0.98	13.0	36
WAM 81.2542	38.5	14.0	13.5	0.96	14.0	36
WAM 83.2708	43.0	16.5	14.8	0.90	16.0	37
WAM 81.2513	86.0	34.0	27.0	0.79	28.0	33

*Remarks.* The marked reduction in rib density with growth characterizes this species and distinguishes it from other *Gunnarites*. *G. denticulatus* (Marshall), revised by Henderson (1970), somewhat resembles *G. raggatti* but its whorl profile with subparallel flanks is different, whorl compression begins later in ontogeny and is not marked, and the rib density increases during ontogeny rather than reducing. *G. varicostatus* Henderson (1970) has comparable shell dimensions but its inner whorls are much less densely ribbed.

*G. raggatti* may be present in Patagonia. The specimen incorrectly assigned to *G. kalika* Stoliczka by Blasco *et al.* (1980) shows the same ontogenetic reduction in rib density and appears to be indistinguishable from the Western Australian species in its other characteristics.

Genus *KOSSMATICERAS* de Grossouvre, 1901

Subgenus *NATALITES* Collignon, 1954

*Kossmaticeras (Natalites) brunschweileri* sp. nov.

Plate 6, figs. 5, 6; Plate 7, figs. 2, 3, 5

*Material.* Holotype WAM 83.2709, locality 23. Paratypes WAM 81.2382, locality 4; WAM 83.1712, locality 16; WAM 83.2710, locality 23; WAM 83.2711, locality 25.

*Description.* Shell widely umbilicate with slightly depressed volutions up to a shell diameter of approximately 35 mm, thereafter becoming more involute with increasingly compressed volutions. Umbilical wall curves outwards to a well-defined umbilical shoulder; flanks are flattened and converge slightly to a well-rounded venter. In juvenile whorls up to a shell diameter of about 40 mm, there are some seven umbilical tubercles per half whorl. Each tubercle gives rise to two to three primary ribs with one to two additional primaries beginning from the umbilical shoulder between tubercles to make a total of twenty to twenty-five ribs per half whorl. More mature growth stages have seven to nine umbilical tubercles per half whorl and a similar arrangement of primary ribs. A few secondaries appear in the mid-flank region and the rib number increases to some thirty-five per half whorl for shell diameters of 60–85 mm. Ribs are thin and weakly flexuous, being prorsiradiate on the dorsal flanks, rectiradiate in the mid-flank area, and very weakly prorsiradiate across the ventral flanks and venter. Five prominent, straight prorsiradiate constrictions per whorl, each truncating two or three ribs. Suture complexly divided with E broad and not quite as deep as the trifold L; U is retracted on the umbilical shoulder and wall.

*Dimensions.*

	D	H	B	B/H	U	%
WAM 81.2382	34.0	11.2	12.0	1.07	15.0	44
WAM 83.2710	42.5	14.5	12.8	0.88	17.2	40
WAM 83.2709	68.5	27.5	20.5	0.74	22.8	33

*Remarks.* The holotype retains areas of well-preserved shell and shows the ribs to be non-crenulate. *K. (N.) brunschweileri* is comparable with *Kossmaticeras (Natalites)* described from south-eastern Africa and recently revised by Kennedy and Klinger (in press) who treat the material as comprising a single, variable species for which *K. (N.) africanus* (van Hoepen 1920) has priority. The African species is distinguished from *K. (N.) brunschweileri* by the more prorsiradiate course of its ribs, especially on the ventral flanks and venter, and its more sinuous constrictions.



*Kossmaticeras (Natalites) sp. (juvenile)*

Plate 7, figs. 4, 5

*Material.* One specimen, locality 23.

*Description.* Shell moderately involute with volutions overlapping by about 50%. Whorls compressed with an outwardly sloping umbilical wall, a clearly defined umbilical shoulder, weakly convex, convergent flanks, and a narrowly arched venter. Some fifteen umbilical bullae per whorl, each generally giving rise to two primary ribs with two or three additional primaries beginning from the umbilical shoulder between adjacent bullae. Sporadic secondaries appear in the mid-flank region so that in all there are some forty-five ribs on the last whorl. All the ribs are thin and separated by interspaces wider than themselves; they swing forward on the dorsal flanks, straighten at the mid-flank, and are very weakly projected across the venter. Five weakly flexuous, prorsiradiate constrictions per whorl, each bordered by collars and truncating three ribs. Suture typical of the *Kossmaticeratidae* with L deep and trifold and U retracted on the umbilical shoulder and wall.

*Dimensions.*

	D	H	B	B/H	U	%
WAM 83.2713	39.2	16.0	12.2	0.76	12.5	32

*Remarks.* The specimen is well preserved, retaining much of its shell. It appears to represent a new species of *Kossmaticeras (Natalites)*, distinguished by its flexuous ribbing and compressed shell form, but more mature growth stages need to be documented before it can be formally named.

## Genus MAORITES Marshall, 1926

*Maorites densicostatus* (Kilian and Reboul, 1909)

Plate 4, figs. 7, 8, 11–13

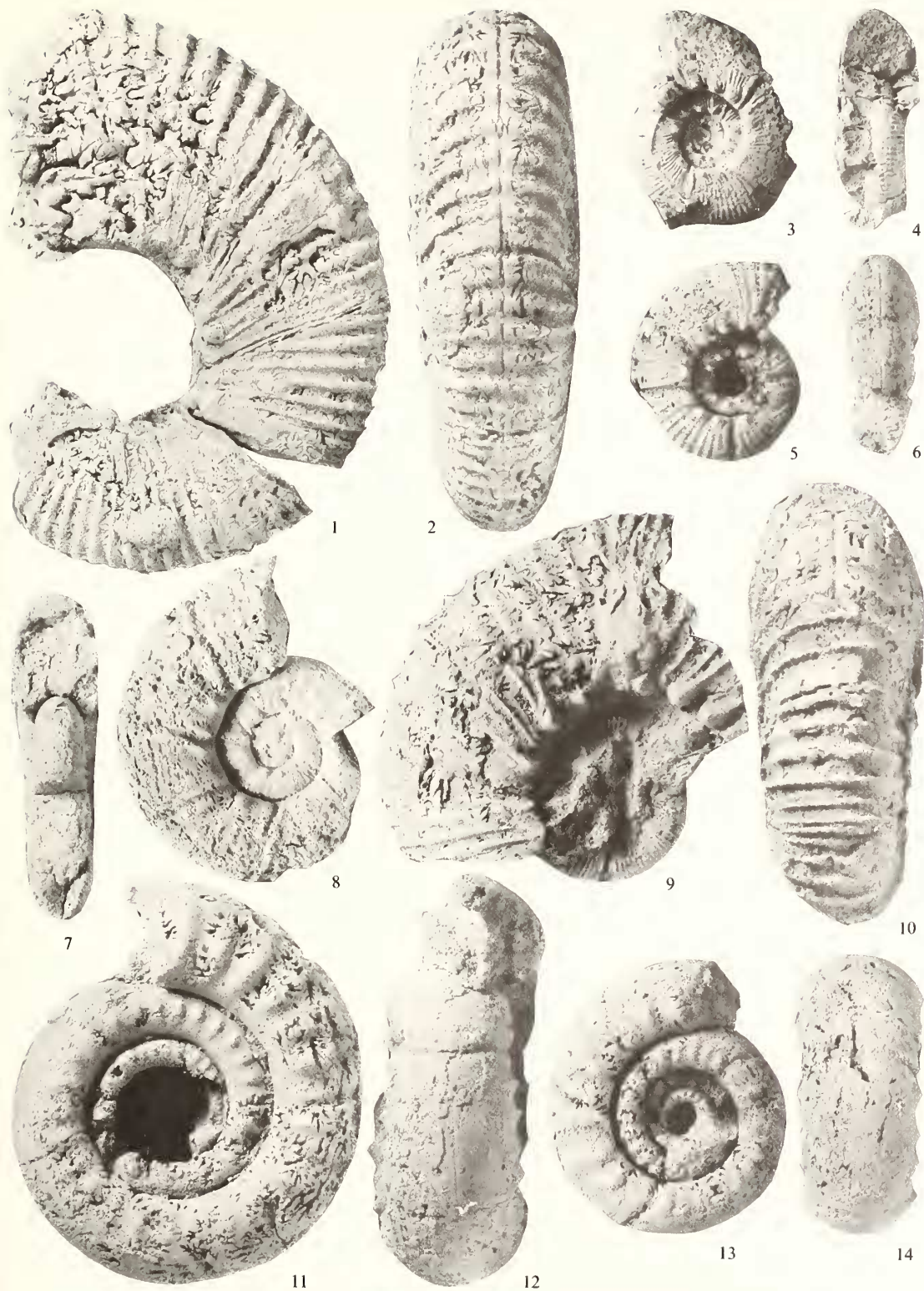
- 1909 *Madrasites bhavaui* (Stoliczka) var. *densicostatus* Kilian and Reboul, p. 30, pl. 15, fig. 4; pl. 18, fig. 1.  
 1964 *Maorites densicostatus* (Kilian and Reboul); Leanza, pl. 1, figs. 6, 7.  
 1965 *Maorites densicostatus* (Kilian and Reboul); Howarth, p. 58, figs. 2d, e, 3c, d.  
 ?1969 *Maorites subtilistriatus* Collignon; Collignon, p. 72, pl. 542, fig. 2124.  
 1977 *Maorites densicostatus* (Kilian and Reboul); Collignon, p. 11, pl. 1, fig. 3; pl. 5, fig. 1.  
 1980 *Maorites tenuicostatus* Marshall; Blasco *et al.*, p. 488, pl. 14, fig. 1.

*Material.* Seventeen specimens, localities 6, 7, 12, 14–18, and 22.

*Description.* Shell compressed, quite strongly so from a diameter of some 40 mm where B/H is 0.64–0.70, and involute, with U measuring some 25% of the post-juvenile shell diameter. Umbilical wall steep but not quite vertical, reflected sharply at the umbilical shoulder into flattened flanks which converge slightly to a narrowly arched venter. Some twenty-six weakly developed, elongate umbilical bullae per whorl, extending down the umbilical wall from the shoulder almost to the umbilical seam. Each gives rise to two or three ribs and an additional rib begins from the shoulder between bullae. Intercalatory ribs, one after every two or three primaries, appear on the mid-flanks. Ribs are prorsiradiate and gently flexuous; they number 145–160 per whorl up to a shell diameter of 50–60 mm and thereafter become coarser and rather more widely spaced. Weakly flexuous, prorsiradiate ribs number six to ten per whorl and each truncates three or four ribs. They are margined

## EXPLANATION OF PLATE 6

- Figs. 1–4, 9–10. *Gunnarites raggatti* sp. nov. 1–2, paratype, WAM 81.2513,  $\times 1$ . 3–4, paratype, WAM 81.2645,  $\times 1$ . 9–10, holotype, WAM 81.2542,  $\times 1$ .  
 Figs. 5–6. *Kossmaticeras (Natalites) brunnschweileri* sp. nov., paratype, WAM 81.2382,  $\times 1$ .  
 Figs. 7–8. *Neograhamites carnarvonensis* sp. nov., holotype, WAM 80.840,  $\times 1$ .  
 Figs. 11–14. *Brahmaïtes (Brahmaïtes) kossmati* sp. nov. 11–12, holotype, WAM 80.786,  $\times 1$ . 13–14, paratype, WAM 82.3083,  $\times 1$ .



by ridges, that on the adapical side being the strongest, and sometimes thickened on the umbilical shoulder and wall to form bullae additional to those which relate to the ribs. Suture typical of the genus, complexly divided even on juvenile shells.

*Dimensions.*

	D	H	B	B/H	U	%
WAM 81.2633	26.5	11.0	8.5	0.77	8.0	30
WAM 81.2633	37.0	15.5	11.0	0.71	9.5	26
WAM 80.847	45.0	19.0	13.0	0.68	11.5	25
WAM 80.1000	53.0	22.5	15.0	0.67	13.0	25
WAM 81.2613	55.0	24.0	15.5	0.64	14.0	25

*Remarks.* The present specimens compare very well with Antarctic Peninsula *M. densicostatus* described by Kilian and Reboul (1909), Spath (1953), and Howarth (1966). Although they are all immature, several show the beginnings of the somewhat coarser ribbing which characterizes *densicostatus* and sets it apart from *M. tenuicostatus* (Marshall) (= *M. suturalis* Marshall) (see Henderson 1970, p. 51). As noted by Howarth (1966), *M. subtilistriatus* Collignon may perhaps be a synonym of *M. densicostatus*. The two species agree in all characteristics, except that *subtilistriatus* has fractionally less compressed whorls (B/H of 0.7–0.74 at shell diameters exceeding 100 mm) than *densicostatus*. Poorly preserved *Maorites* resembling *subtilistriatus* are recorded from southern Africa by Kennedy and Klinger (in press).

A close morphological similarity between *M. densicostatus* and finely ribbed *Gunnarites bhavaniformis* Kilian and Reboul (= *G. kalika* Spath non Stoliczka) was observed by Spath (1953) and Howarth (1966) for Antarctic Peninsula material. In the Western Australian collections, *M. densicostatus* and *G. kalika* (Stoliczka) are indistinguishable in shell dimensions, whorl profile, and the density of ribbing. Save for rib crenulation, which is indeterminable for many specimens due to imperfect shell preservation, individuals of the two species can only be separated by the nature of umbilical bullae which are consistently much stronger and less elongate in *G. kalika*.

It is tempting to suggest that *M. densicostatus* was derived from a finely ribbed *Gunnarites* like *G. kalika*, in Campanian time, by the loss of rib crenulation and slight modification to the ornament. However, *Maorites* (including *M. subtilistriatus*) were already speciated in the lower Campanian of Madagascar (Collignon 1955b, 1969). It may be that finely ribbed, compressed kossmaticeratids were derived from more than one ancestral stock and that *Maorites* is a polyphyletic grouping.

Genus GROSSOUVRITES Kilian and Reboul, 1909

*Grossouvrites gemmatus* (Huppé, 1854)

Plate 5, figs. 1–7

1854 *Ammonites gemmatus* Huppé, in Gay, p. 35, pl. 1, fig. 3.

1958 *Grossouvrites gemmatus* (Huppé); Howarth, p. 12, pl. 2, fig. 4a, b.

1965 *Grossouvrites gemmatus* (Huppé); Hünicken, p. 77, pl. 6, figs. 1, 2; pl. 7, figs. 8, 9.

*Material.* Eighteen specimens, localities 5, 9, 12, 15–20, 23, and 25.

*Description.* Juvenile growth stages, up to a shell diameter of about 30 mm, are evolute, the umbilicus measuring about 35% of the shell diameter, and have an equidimensional whorl profile. Later growth stages become involute, the umbilicus reducing to some 26% of the shell diameter, and are slightly compressed. Umbilical wall steep but not vertical, sharply turned at the umbilical shoulder into weakly convex flanks which converge slightly towards a broadly rounded venter. There are some twenty-two small, regularly spaced umbilical tubercles per whorl, each giving rise to one or two ribs, with an additional rib beginning at the umbilical shoulder between tubercles. Secondary ribs, one after each primary, begin from the mid-flank region so that about 100 ribs are present on each whorl. Primaries have a slight prorsiradiate inclination on the dorsal flanks but, like the secondaries, are straight and rectiradiate on the ventral flanks and very weakly projected on the venter. Constrictions are restricted to juvenile growth stages with shell diameters of less than 35 mm. Each is margined on both sides by collars, that on the adapertural side being slightly the stronger. They are almost straight with a slightly prorsiradiate inclination on the flanks and weakly projected on the venter; each truncates one or two



ribs. The suture is very fine divided, even at juvenile growth stages at shell diameters less than 10 mm, unusually so for a kossmaticeratid. L is deeper than E and trifid; U is retracted and on the umbilical wall.

#### Dimensions.

	D	H	B	B/H	U	%
WAM 81.2634	30.0	12.0	12.0	1.00	10.5	35
WAM 10574	44.5	19.0	16.5	0.87	13.5	30
WAM 81.2521	55.0	25.0	19.5	0.78	15.0	27
WAM 83.2690	64.5	31.2	24.8	0.79	16.8	26
BM C49087	c. 66.0	34.8	28.0	0.80	16.8	c. 25
WAM 83.2689	91.0	41.0	29.8	0.73	22.5	25
WAM 83.2691	100.5	44.0	31.5	0.72	25.5	25

*Remarks.* The Western Australian specimens are identical in shell dimensions and other characters with the Antarctic Peninsula specimen (BM C49087) figured by Howarth (1958) and the original of Kilian and Reboul's 1909, pl. 17, fig. 2a, b of which the British Museum (Natural History) holds a cast (C23232). The type specimen illustrated by Huppé is a little more compressed with a whorl breadth/whorl height ratio of about 0.76 at a shell diameter of about 40 mm. However, the specimens measured by Steinmann (1895) and Hünicken (1965) are considerably more compressed with whorl breadth/whorl height ratios of 0.61 and 0.51 respectively; presumably they are crushed.

The large fragment of body chamber figured by Spath (1953, pl. 5, fig. 1a, b) shows that the same style of ornament persists to a late stage of growth where the shell diameter is more than 180 mm.

#### Genus BRAHMAITES Kossmat, 1897

##### Subgenus BRAHMAITES

1897a *Brahmaites* Kossmat, p. 44.

*Type species.* *Anmonites brahma* Forbes, 1846, p. 100, pl. 8, fig. 1.

*Remarks.* *Brahmaites* of current interpretation comprises a loosely knit group of Maastrichtian kossmaticeratids characterized by evolute shells with inflated whorls lacking a clear umbilical shoulder and with ribbing effaced or absent, at least in early growth stages. Siphonal tubercles are present at late growth stages.

The type species, *B. brahma* (Forbes) from Pondicherry, southern India, is represented by a substantial suite of specimens held by the British Museum (Natural History), including Forbes's type series. All growth stages are represented, to a shell diameter of 108 mm. The whorls are depressed throughout ontogeny, strongly so when juvenile where the whorl breadth/whorl height ratio ranges up to 2.04. Ornament consists of numerous umbilical bullae which disappear at a shell diameter of about 70 mm, annular ribs that first appear at a shell diameter of about 60 mm, and infrequent constrictions preceded by prominent collars which bear siphonal tubercles at a late stage of growth. A closely related species, *B. kossmati* sp. nov., is established below for Western Australian material. Specimens from Madagascar described by Collignon (1938, 1971), and from Otacod, southern India, described by Kossmat (1897a) were originally referred to *B. brahma* but may represent other species. All of these forms comprise a closely related species group whose geographic range was restricted to the Indian Ocean.

A second species group may be recognized, of which the southern Indian *B. vishu* (Forbes) is the best-known example. This species has equidimensional to weakly compressed whorls bearing simple annular ribs which are weak on initial growth stages but become widely spaced and strong, with siphonal tubercles, later in ontogeny. Umbilical tubercles are lacking. Included here is the French *B. haugi* (Seunes, 1891) (= *Gaudryceras planorbiforme* Grossouvre, 1894, non Böhm 1891), *B. sachalinensis* Yabe and Shimizu, 1924 from Saghalien, and probably *B. nikobokensis* Collignon, 1971 from Madagascar. Additional records are of *B. vishnu* from Armenia (Atabekian and Akopian 1970) and *B. haugi* from Madagascar (Collignon 1938). Besides a different morphology, this species group has a much wider distribution than *Brahmaites* (s.s.). It seems worthy of subgeneric

segregation for which *Anabrahmaites*, with *A. vishnu* (Forbes) as its type species, has already been introduced by Yabe and Shimizu (1924, p. 79).

The juvenile *B. haugi* (Seunes), recorded from Spain by Wiedmann (1969, pl. 3, fig. 4), is too small and poorly preserved to be given a generic assignment and *B. rotundus* Marshall, 1926 is now known to be a juvenile *Jacobites* (*J.*) *nodulosus* (Marshall) (see Henderson 1970, p. 42).

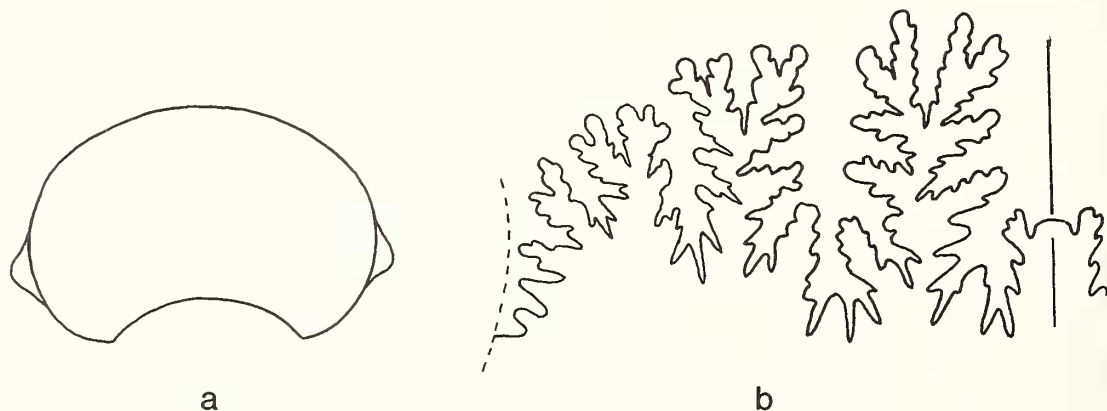
*Brahmaites* (*Brahmaites*) *kossmati* sp. nov.

Plate 6, figs. 11–14; Plate 7, fig. 1; text-figs. 9a, b, 10

?1897a *Brahmaites brahma* (Forbes); Kossmat, p. 45 *pars*, pl. 8, fig. 7a, b

*Material.* Holotype WAM 80.786, locality 10. Paratypes WAM 82.3083, locality 5; WAM 80.964, 83.2697, 83.2700, locality 12; WAM 83.2698, 83.2699, locality 25.

*Description.* Shell serpenticonic with the umbilicus measuring about 50% of the shell diameter. Whorls strongly depressed with a B/H ratio of 1.6–1.8 at a shell diameter of 50 mm, increasing to more than 2.0 in the initial growth stages. Convex, outwardly sloping umbilical wall merges imperceptibly with convex flanks so that no umbilical shoulder is defined; the venter is broadly arched. Prominent, radial umbilical bullae number twenty-two to twenty-six per whorl. Up to a shell diameter of 55 mm they extend for a short distance on to the flanks but at later growth stages, up to a shell diameter of approximately 70 mm, they extend further, reaching across the flanks to the edge of the venter. For a final growth stage the ribs continue their rectiradial course across the venter and become much stronger. Here they merge imperceptibly with the umbilical bullae and some lack bullae completely. Irregularly spaced constrictions, numbering three to five per whorl, are rectiradial on the umbilical wall, swing gently forward on the flanks, and are projected on the venter. They are bordered by collars of which the strongest is that positioned adapically which develops a siphonal tubercle at a shell diameter of approximately 70 mm. Suture of kossmaticeratid plan but not complexly divided. L is asymmetrically trifold and only slightly deeper than E, U is retracted on the umbilical wall, and I is trifold.



TEXT-FIG. 9. *Brahmaites kossmati* sp. nov. a, whorl profile, paratype, WAM 80.964,  $\times 2$ . b, suture, holotype, WAM 80.786,  $\times 4$ .

EXPLANATION OF PLATE 7

Fig. 1. *Brahmaites* (*Brahmaites*) *kossmati*, sp. nov., paratype, WAM 83.2697,  $\times 1$ .

Figs. 2–3. *Kossmaticeras* (*Natalites*) *brunnschweileri* sp. nov., holotype, WAM 83.2709,  $\times 1$ .

Figs. 3, 4. *Kossmaticeras* (*Natalites*) sp. juv., WAM 83.2713,  $\times 1$ .

Fig. 5. *K. (N.) brunnschweileri*, paratype, WAM 83.2710,  $\times 1$ .

Fig. 6. *Pachydiscus* (*Pachydiscus*) *neubergicus dissitus* subsp. nov., holotype, WAM 83.2694,  $\times 1$ .



HENDERSON and McNAMARA, Kossmaticeratidae and Pachydiscidae

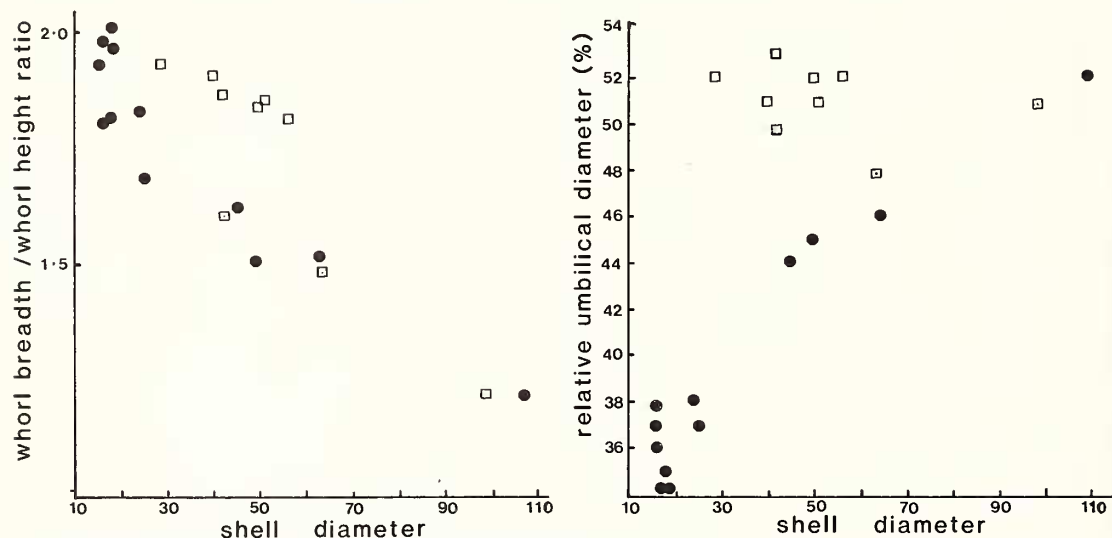


*Dimensions.*

	D	B	H	B/H	U	%
WAM 81.3083	28.0	14.0	7.2	1.94	14.5	52
WAM 80.964	40.0	18.0	9.5	1.90	20.5	51
WAM 81.3083	42.0	19.0	10.2	1.86	22.2	53
WAM 83.2700	42.2	19.0	11.8	1.61	21.0	50
WAM 80.964	50.0	23.0	12.5	1.84	26.0	52
WAM 80.786	51.0	18.5	10.0	1.85	26.0	51
WAM 80.786	56.0	24.5	13.5	1.81	29.0	52
WAM 83.2698	62.8	26.0	17.5	1.49	30.0	48
WAM 83.2697	98.8	36.5	29.8	1.22	50.5	51

*Remarks.* WAM 83.2697 probably represents a mature specimen as it has three-quarters of a whorl of body chamber terminated by a prominent constriction. None of the specimens shows the inception of the adult ornament but its development is almost certainly gradual with the ribs extending progressively further across the flanks and on to the venter.

*B. (B.) kossmati* is closely related to *B. brahma* (Forbes). Juveniles of *kossmati* are distinguished by being more widely umbilicate and tend to have more depressed volutiones (text-fig. 10). When adult, *kossmati* has stronger, more numerous ribs than its Indian ally.



TEXT-FIG. 10. Plots of whorl breadth/whorl height and umbilical diameter expressed as a percentage of the shell diameter showing ontogenetic trends for *Brahmaites (B.) brahma* (Forbes) (dots) and the separation of *Brahmaites (B.) kossmati* sp. nov. (squares). Abscissa scales are in millimetres.

The status of the two specimens from Otacod, southern India, figured by Kossmat (1897a, pl. 8, figs. 7a, b, 8a-c) as *B. (B.) brahma*, is uncertain. The ribbed juvenile is definitely not of this species as several of the British Museum (Natural History) juveniles from the type series of *brahma* retain their shell and show the test surface to be smooth. The larger specimen, with a shell diameter of 88 mm, appears to be more like *B. (B.) kossmati* in shell form and in ornament but does not develop the mature ribbing. The status of *B. (B.) brahma* recorded by Collignon (1938, 1971) is also in doubt. Collignon's measurements show the Madagascan specimens to be much more slender whorled than the Pondicherry types, with whorl breadth/whorl height ratios of about 1.2 at shell diameters of 50–80 mm. Perhaps they represent a local species, but it may be noted that a Pondicherry specimen measured by Stoliczka (1865) was reported as being equally slender whorled.

Whereas adult kossmaticeratids as a whole tend to be involute with equidimensional or compressed whorl profiles, the evolute coiling and depressed whorl profile shown by *B. (B.) kossmati* and *B. (B.) brahma* are typical of many juveniles. For example, measurements of ontogenetic series for New Zealand kossmaticeratids show this trend for *J. (J.) nodulosus* (Marshall) and *Gunnarites spathi* Henderson (see Henderson 1970). Indeed a juvenile of the former was mistakenly referred to *Brahmaites* by Marshall (1926). Effacement and eventual loss of ornament and simplification of the suture is typical of kossmaticeratids, like all ammonites, as the initial whorls are followed back towards the apex. It may well be that *Brahmaites (Brahmaites)* is the Maastrichtian result of paedomorphic derivation from a more typical Campanian kossmaticeratid stock.

### Genus NEOGRAHAMITES Spath, 1953

*Type species. Neograhamites kiliani* Spath, 1953.

*Remarks.* *Neograhamites* is characterized by an evolute shell form with a low, outwardly sloping umbilical wall, subdued ornament of umbilical tubercles, and straight, rectiradiate ribs except for a final stage of growth where coarse ribs prevail. It is closely allied to *Pseudokossmaticeras* Spath 1922, from which it differs only in having fewer, more distinct umbilical tubercles to which ribs join in pairs rather than singly. The late growth stage coarsening of the ribs displayed by *N. kiliani* is also shown by some *Pseudokossmaticeras*—for example, *P. galicianum* (Favre) as figured by Błaszkiwicz (1980, pl. 54, fig. 1).

In addition to the type species, *N. taylori* Spath also from the Antarctic Peninsula was included in the genus at its establishment, and a further species, *N. transitorius* Henderson (1970) added from New Zealand. However, both of these species are much more involute than *N. kiliani* or *N. carnarvonensis* from Western Australia (established herein), with higher, steeper umbilical walls and strong umbilical tubercles. The same observations are true for the Patagonian specimens described by Blasco *et al.* (1980) as *Neograhamites* aff. *taylori* Spath. *N. transitorius* is more satisfactorily placed in *Kossmaticeras (Natalites)* Collignon, 1955*b* whereas the somewhat effaced ribbing on the dorsal flanks of *N. taylori* suggests reference to *Kossmaticeras (Karapadites)* Collignon, 1954.

*Holcodiscus hauthali* Paulcke (1906) was compared with *Neograhamites* by Matsumoto (1955) and by Theidig and Wiedmann (1976). It presumably is the basis of the record of *Neograhamites* from Patagonia given by Arkell, Kummel and Wright (1957). Leanza (1967) referred this species to *Pseudokossmaticeras*. However, its degree of involution, steep umbilical wall, and flexuous ribs show that it is not closely related to either of these genera. It resembles *N. transitorius* Henderson and should likewise be transferred to *Kossmaticeras (Natalites)*.

*Neograhamites* as interpreted here comprises but two species, and is known only from the Antarctic Peninsula and Western Australia. Its range is ?upper Campanian–Maastrichtian.

### *Neograhamites carnarvonensis* sp. nov.

Plate 6, figs. 7, 8

*Material.* Holotype WAM 80.840, locality 9.

*Description.* Shell discoidal, evolute, with compressed whorls. Umbilical wall low, vertical at the umbilical seam but convex and sloping outwards to pass smoothly into the flanks such that the umbilical shoulder is rather poorly defined. The flanks are somewhat flattened and very slightly convergent, the venter narrowly rounded. Six or seven straight, prorsiradiate constrictions per whorl, bordered by collars which are sometimes raised into very weak bullae as they cross the umbilical shoulder. Some nine stronger umbilical bullae per whorl lying between the constrictions are not as well marked on the last whorl as on that preceding it. Some thirty-six straight, rectiradiate ribs per whorl, most arising in pairs from the umbilical bullae or from the umbilical wall between tubercles. Two ribs preceding each constriction are truncated. Suture kossmaticeratid in style and quite complexly divided. L is considerably deeper than E, which is asymmetrically trifid; U is retracted on the umbilical wall.

*Dimensions.*

	D	H	B	B/H	U	%
WAM 80.840	49.0	16.5	13.5	0.82	20.0	41

*Remarks.* *N. carnarvonensis* compares closely with *N. kiliani* Spath (1953), differing only in having a more compressed whorl section with subparallel flanks and a broadly rounded venter. The unique holotype of the Antarctic species, BM C41366, has a whorl breadth/whorl height ratio of 0.94. Even weakening of the umbilical tubercles at a shell diameter of 35–40 mm is a shared feature. The change in ornament to sparse, coarse ribs shown by *N. kiliani* occurs at a shell diameter of some 55 mm and represents a later stage of growth than those shown by the holotype of *N. carnarvonensis*.

## Family PACHYDISCIDAE Spath, 1922

## Genus PACHYDISCUS Zittel, 1884

1884 *Pachydiscus* Zittel, p. 466.

1900 *Parapachydiscus* Hyatt, p. 570.

1958 *Joaquinites* Anderson, p. 218.

*Type species.* *Pachydiscus* (*P.*) *neubergicus* (von Hauer, 1858).

*Remarks.* *Pachydiscus* is an important genus for Campanian and Maastrichtian correlation whose potential has not been fully realized due to inadequate knowledge of its species. Most records of the genus have been based on a small number of specimens for which a full ontogeny cannot be documented nor intraspecific variation determined. In addition, several important species were first described in the middle of the last century and were based on inadequate types, illustrated by hand, and their type series have not as yet been adequately revised. As a result, the classification of *Pachydiscus* species, especially those from Europe, is perhaps less well understood than that of any other upper Cretaceous genus. The three Western Australian species are all present in Europe and are represented by sufficient material to permit a substantially complete documentation of their morphology, thereby resolving some of the conflict in the European literature.

In contrast to the other two species, generic placement of *P. fresvillensis* Seunes is somewhat arbitrary. Its depressed immature volutions and relatively coarse ribbing suggest reference to *Eupachydiscus* Spath, 1922, but its weakly compressed adult whorls with flattened, convergent flanks and the eventual restriction of ribbing to the ventral flanks and venter are characteristics of *Pachydiscus*. It is retained in *Pachydiscus*, thereby conforming with the previous literature. Two subgenera are recognized within *Pachydiscus*, distinguished by the nature of mature ornament. *Pachydiscus* (*Pachydiscus*) retains ribbing whereas it is lost from late growth stages of *P. (Neodesmoceras)* Matsumoto, 1947.

## Subgenus PACHYDISCUS

*Pachydiscus* (*Pachydiscus*) *neubergicus dissitus* subsp. nov.

Plate 7, figs. 7, 9; Plate 10, figs. 3–6; text-figs. 11, 12c, 13c

1941 *Pachydiscus* aff. *gollevillensis* (d'Orbigny); Spath, p. 45, pl. 2, fig. 1a, b.

*Material.* Holotype WAM 83.2694, locality 15. Paratypes UWA 20139, WAM 60.105, locality 1; WAM 81.2555, locality 5; WAM 60.54, 60.75g, 71.210, 80.838, locality 7; WAM 80.963, locality 12; WAM 81.2540, 83.2695, locality 16; WAM 83.2696, locality 17. Six additional specimens, localities 12, 16, 17, and 25.

*Description.* Shell compressed and involute, with a whorl breadth/whorl height ratio of 0.75–0.78 and an umbilicus which measures 26–28 % of the shell diameter. Umbilical wall inclined outwards, turning gently at the umbilical shoulder into weakly convex, slightly convergent flanks. Venter narrow, evenly rounded. Primary ribs, numbering about eleven per whorl, begin at a shell diameter of some 25 mm and extend from the umbilical seam to the mid-flanks. They are faint and rursiradiate on the umbilical wall but become rectiradiate on the dorsal flanks where they swell to form elongate umbilical bullae. Secondary ribs, confined to the ventral flanks and venter, begin at a shell diameter of 40–45 mm. They number twenty-three to twenty-five per half whorl up to a





TEXT-FIG. 11. *Pachydiscus (Pachydiscus) neubergicus dissitus* subsp. nov., paratype, WAM 81.2555,  $\times 1$ .

shell diameter of 85–95 mm, thereafter becoming much more closely spaced and a little weaker. Their course is almost straight and slightly prorsiradiate, and they become generally stronger across the venter except on the mid-ventral line where they are slightly effaced. Some primary ribs are out of phase with the secondaries, being separated from them by a slight mid-flank gap. Suture typical of the genus, with U strongly retracted on the umbilical wall.

#### Dimensions.

	D	H	B	B/H	U	%
WAM 81.2540	43.2	18.5	14.2	0.76	11.2	26
WAM 60.75g	49.0	21.0	15.8	0.75	12.5	26
WAM 80.963	56.5	24.0	18.8	0.78	15.0	27
WAM 60.105	66.0	28.0	21.0	0.75	18.5	28
WAM 71.210	80.0	33.0	25.2	0.76	21.2	27
WAM 83.2696	92.8	40.0	29.2	0.73	25.5	27
WAM 83.2694	122.5	51.5	37.0	0.72	32.2	26

**Remarks.** The growth stage at which the fine, mature ornament first appears is somewhat variable. It commences at a shell diameter of 95 mm on the holotype (WAM 83.2694), but is absent from WAM 83.2696 at an equivalent diameter which represents the last preserved growth stage of that specimen. On UWA 20139, the specimen figured by Spath (1941, pl. 2, fig. 1a, b), fine ribbing appears at a shell diameter of 85 mm. Mature secondary ribs number about twenty-five per quarter whorl. The holotype consists entirely of phragmocone so that the adult ornament must have characterized most of the last whorl of a complete, fully grown shell.

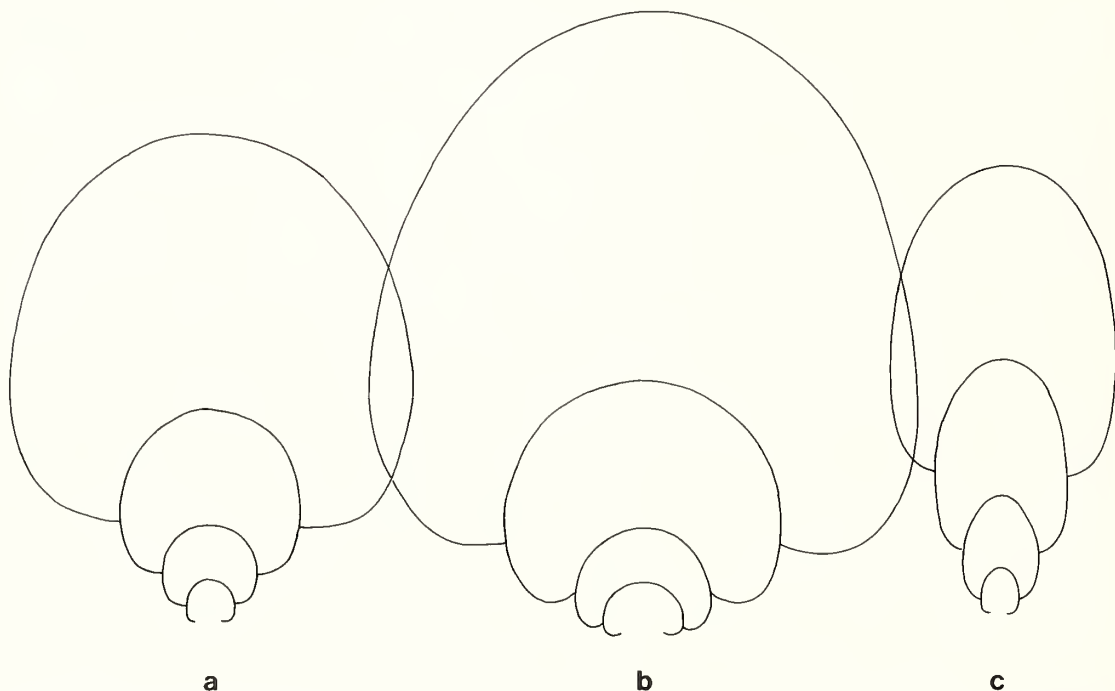
*P. (P.) neubergicus* (von Hauer) is here regarded as a synonym of *P. (P.) chrishna* (Forbes). Separation of these two species is no doubt largely due to the original hand-drawn illustrations, those of Forbes (1846, pl. 9, fig. 2a, b) accentuating effacement of ornament on *chrishna* whereas those of von Hauer (1858, pl. 2, figs. 1–3) displayed *neubergicus* as having strong ornament. A comparison of the unique holotype of *chrishna* (BM C51041) with photographs of the type series of

*neubergicus* (W. J. Kennedy, unpublished) shows the distinction to be much more subtle than the original illustrations suggest. The photographs of the *neubergicus* types and the holotype of *chrishna* show a change to mature ornamentation at a shell diameter of 8–9 cm where secondary ribs disappear and the primaries extend across the flanks to the margin of the venter, the bullae becoming more elongated and less clearly defined. A large French specimen of *neubergicus* figured by de Grossouvre (1894, pl. 30, fig. 4a, b) has similar adult ornament except that the primary ribs strengthen and become more widely spaced.

The synonymy of *P. (P.) Neubergicus* (von Hauer 1858) and *P. (P.) chrishna* (Forbes 1846) cannot be satisfactorily resolved by application of the rule of priority. The name *neubergicus* is entrenched in the literature, having been used for this species in descriptions and lists from many European localities. It has, in addition, been used as the name of a lower Maastrichtian zonal index species for nearly ninety years. In contrast no specimens other than Forbes's unique holotype have been described or listed as *P. (P.) chrishna*. In consequence, Henderson and Kennedy (in press) have applied to the International Commission on Zoological Nomenclature to suppress *chrishna* in favour of *neubergicus*.

The Western Australia suite is assigned to a new subspecies, *P. (P.) Neubergicus dissitus*, because its mature ornament is different from that of von Hauer's type series of *neubergicus* (s.s.) and other specimens referred to the species. Its earlier growth stages, however, are indistinguishable from European *neubergicus*, such as those illustrated by Schlüter (1872) and Błaszkiwicz (1980), and differ from Forbes's original of *chrishna* only in displaying slightly stronger ribs.

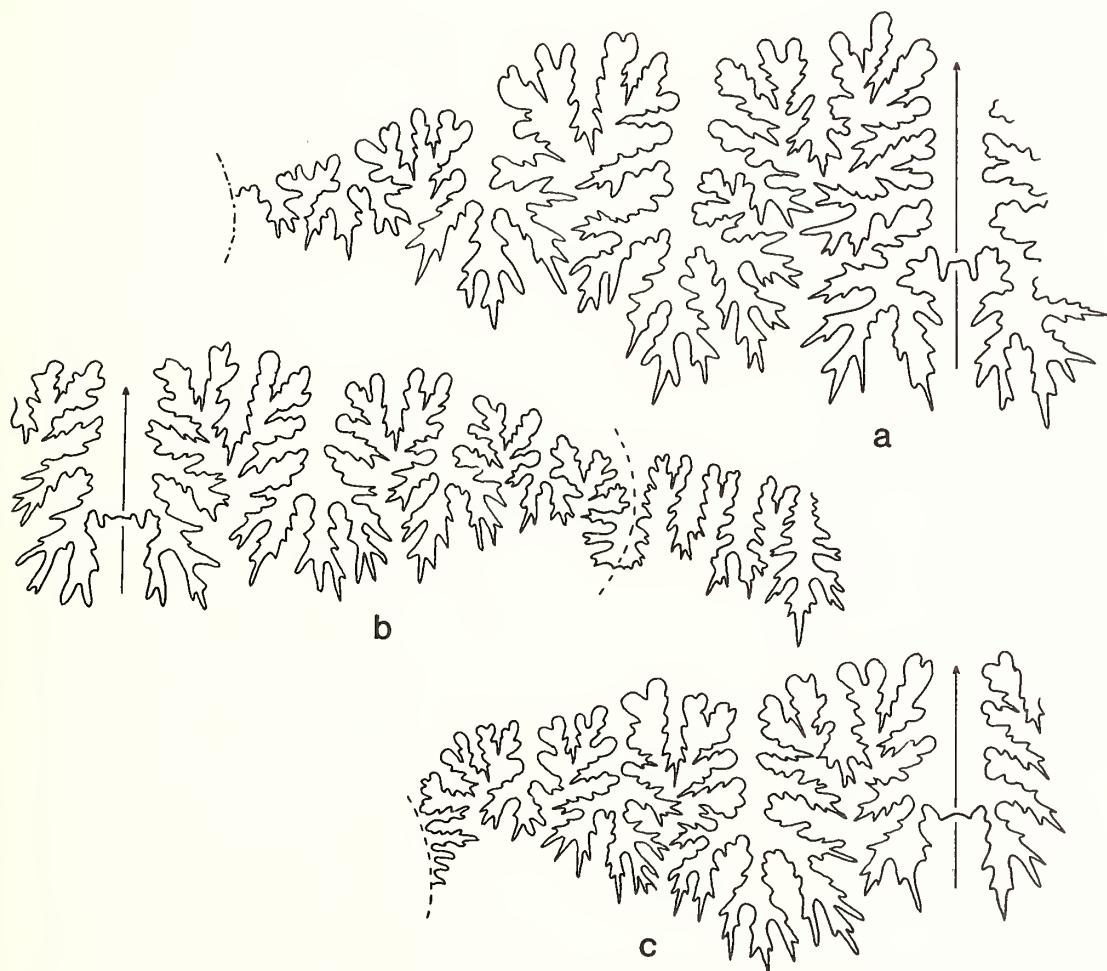
*P. (P.) Neubergicus dissitus* may be regarded as a morphological intermediate between *neubergicus* (s.s.) and *P. (P.) gollevillensis* (d'Orbigny, 1850). These two species differ only in the density of secondary ribs, which number sixty to seventy per whorl for *gollevillensis* compared with forty-five to



TEXT-FIG. 12. Whorl profiles of *Pachydiscus* (*Pachydiscus*). a, *P. (P.) jacquoti australis* subsp. nov., drawn from paratypes WAM 81.2454 and WAM 81.2529. b, *P. (P.) fresvillensis* Seunes, WAM 2527, c, *P. (P.) Neubergicus dissitus* subsp. nov., drawn from paratypes WAM 80.963 and WAM 81.2555. All  $\times 10$ .

fifty per whorl for *neubergicus*. They have been often confused in the literature and Atabekian and Akopian (1969) considered them as subspecies of *gollevillensis* (*s.l.*). The mature ornament of *P. (P.) Neubergicus dissitus* is very similar to that of *gollevillensis* (see Pl. 7, fig. 7; Pl. 9, figs. 5, 6) and evolution of the former to the latter could have been effected by accelerating the onset of fine secondary ribbing to an earlier stage of ontogeny.

*P. perfidus* de Grossouvre (1894, p. 213, pl. 34, fig. 1) has inner whorls like those of *P. Neubergicus* but the adult ornament consists of coarse primaries which are strongly marked on the venter where they are separated by occasional intercalated secondaries of equal strength. Polish specimens referred to a new subspecies of *P. (P.) Neubergicus*, *P. (P.) Neubergicus raricostatus*, and to *P. perfidus* by Blaszkiewicz (1980) have similar adult ornament, as does the specimen figured by de Grossouvre (1894, pl. 38, fig. 3) as *P. Neubergicus*. The status of these forms is equivocal because no reliable shell dimensions have been published, save for a whorl profile drawn by de Grossouvre (1894, superimposed on pl. 38, fig. 3) which suggests a whorl breadth/whorl height ratio of 0.9.



TEXT-FIG. 13. Sutures of *Pachydiscus* (*Pachydiscus*). a, *P. (P.) fresvillensis* Seunes, WAM 80.785. b, *P. (P.) jacquoti australis* subsp. nov., paratype, WAM 81.2352. c, *P. (P.) Neubergicus dissitus* subsp. nov., paratype, WAM 60.105. All  $\times 3$ .



*P. (P.) neubergicus* has been widely regarded as an index species of the lower Maastrichtian in Europe (see, for example, Arkell, Kummel and Wright 1957; Wiedmann 1979). It also occurs in the Maastrichtian of Armenia and India as well as in Western Australia.

*Pachydiscus (Pachydiscus) jacquoti australis* subsp. nov.

Plate 8, figs. 1, 2, 7–10; text-figs. 12a, 13b, 14, 15a

1941 *Pachydiscus* sp. nov.? Spath, p. 46.

**Material.** Holotype WAM 80.1004, locality 12. Paratypes WAM 81.2431, 81.2454, 81.2352, locality 4; WAM 81.2525, 81.2529, 82.3082, locality 5; WAM 71.213, 81.2708, 81.2711, NMV P31024, locality 6; WAM 60.76f, locality 7; WAM 80.827, 80.836, locality 9; WAM 80.783, locality 10; WAM 80.981, locality 12; WAM 81.2639, locality 15. One hundred and forty-two additional specimens, localities 1, 2, 4–13, 15–21, 23, 25, and 26.

**Description.** Shell large, the umbilical width ranging from 22 to 28% of the shell diameter. Whorls nearly equidimensional to slightly depressed, whorl breadth/whorl height ratios ranging from 0.96 to 1.19, widest on the dorsal flanks. Umbilical wall vertical at its base but curving outward to pass smoothly into gently rounded umbilical shoulder. Flanks weakly convex, and slightly convergent; the venter is broadly arched. Broad primary ribs appear at a shell diameter of less than 10 mm and increase quickly in number to ten to twelve per whorl. They are very weak and rursiradiate on the umbilical wall, strengthen on the dorsal flanks where they are rectiradiate and form elongate bullae, and weaken on the mid-flank region. Broad secondary ribs, confined to the ventral flanks and venter, appear at a shell diameter of 45–55 mm. They are rectiradiate or weakly prorsiradiate, weaken noticeably on the mid-ventral line, and number thirty to thirty-six per whorl. Primary ribs pass into one or two secondaries in the mid-flank region but often with an offset junction suggesting that the two rib sets are slightly out of phase. At a shell diameter of about 145 mm, the primaries disappear and the secondaries become slightly weaker. The suture is typical of the genus; florid with L and I deeply incised and trifid, and U retracted on the umbilical wall.

**Remarks.** The largest specimen is a septate whorl fragment, showing weak secondary ribs at a whorl height of 10.5 cm, which corresponds to a shell diameter of some 25.5 cm. Shell dimensions (text-fig. 14) show no detectable ontogenetic change in whorl proportions but the relative umbilical diameter decreases slightly with growth. The spread in relative whorl breadth is in part an artefact, some measurements having been taken on the crests of bullae whereas others were taken between bullae. Umbilical tubercles vary in strength both on individual specimens and between specimens, being compact and strong at one extreme and elongate and weak at the other. In some specimens the secondary ribs are quite strong on the margins of the venter but disappear on the ventral midline so that they have the appearance of weak ventrolateral bullae. On others they are only slightly weakened on the ventral midline.

*P. (P.) jacquoti* is known from France (Seunes 1890, 1891) and has been described from British Columbia (Usher 1952), Armenia (Atabekian and Akopian 1969), and Madagascar (Collignon 1971). It has at times been confused with *P. (P.) neubergicus* (von Hauer) but the Western Australian collections show that the two species are quite separate. *P. (P.) neubergicus* is set apart by its more compressed whorl profile and more closely spaced secondary ribs. The specimen figured by de Grossouvre (1894, pl. 26, fig. 3a, b) and Collignon (1938, pl. 8, fig. 4, 4a, 4b) as *neubergicus* are better placed in *jacquoti*.

The type series of *P. (P.) jacquoti* (Seunes 1890, p. 5, pl. 2, figs. 1a, b, 3a, b) is indistinguishable from the Western Australian suite up to shell diameters of 8 cm. However, a difference is apparent in

---

EXPLANATION OF PLATE 8

Figs. 1–2, 7–10. *Pachydiscus (Pachydiscus) jacquoti australis* subsp. nov. 1–2, paratype, WAM 82.3082,  $\times 1$ . 7–8, paratype, WAM 81.2431,  $\times 1$ . 9–10, paratype, WAM 81.2639,  $\times 1$ .  
Figs. 3–6. *Pachydiscus (Pachydiscus) fresvillensis* Seunes. 3–4, NMV P31024,  $\times 1$ . 5–6, WAM 60.761,  $\times 1$ .



HENDERSON and McNAMARA, *Pachydiscus* (*Pachydiscus*)

mature ornamentation. Whereas the Western Australian specimens retain secondary ribs at all known stages of growth (text-fig. 14) up to a shell diameter of 25 cm, they disappear at a shell diameter of 8 cm on the French types. Accordingly the Western Australian suite is segregated as a subspecies. *P. (P.) egertoni* (Forbes 1846, p. 108, pl. a, fig. 1a-c) is a close ally of *P. (P.) jacquoti*, differing only in its more effaced ornament and the more distinctly convergent flanks of later whorls. Its juvenile growth stages, described by Forbes (1846, p. 103, pl. 7, fig. 8a-c) as *Ammonites ganesa*, also show effaced ribbing and have fewer umbilical bullae than those of *P. (P.) jacquoti*. The status of other Indian specimens figured by Stoliczka (1864, pl. 15, fig. 4a-c) and Kossmat (1898, p. 15, fig. 4a-c) as *P. (P.) egertoni* is uncertain. They are more strongly ornamented than Forbes's type series (BM C51038 and C51043) and may well represent *P. (P.) jacquoti*.

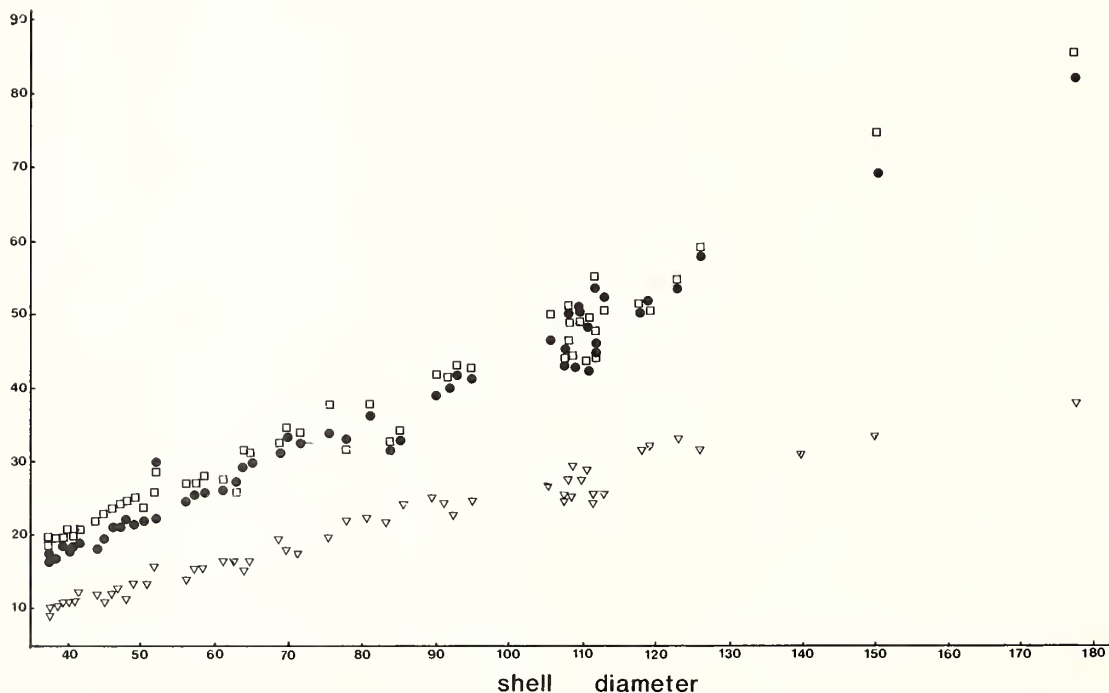
Other *Pachydiscus* species of similar morphology include *P. (P.) colligatus* (van Binkhorst, 1861), *P. (P.) epiplectus* (Redtenbacher, 1873), *P. (P.) fresvillensis* Seunes, 1890, and *P. (P.) subrotundus* Seunes, 1890. They are distinguishable from *P. (P.) jacquoti* by the nature of the ribs which all begin from the umbilical wall or dorsal flanks so that secondary ribs cannot be discriminated.

French *P. (P.) jacquoti* are of Maastrichtian age but the species also occurs in the Pender Formation, British Columbia (Usher 1952), which is of Campanian age (Ward 1978).

*Pachydiscus (Pachydiscus) fresvillensis* Seunes, 1890

Plate 8, figs. 3-6; Plate 9, figs. 1, 2; text-figs. 12b, 13a, 15b

- 1865 *Ammonites arrialoorensis* Stoliczka, p. 126 *pars*, pl. 63, fig. 2, 2a (*non* pl. 63, fig. 3, 3a; pl. 64, fig. 1, 1a).  
 1890 *Pachydiscus fresvillensis* Seunes, p. 3, pl. 1, fig. 1a, b.  
 1891 *Pachydiscus fresvillensis* Seunes; Seunes, p. 14, pl. 3, fig. 1a, b.



TEXT-FIG. 14. Shell dimensions of *Pachydiscus (Pachydiscus) jacquoti australis* subsp. nov. Squares represent whorl breadth, dots represent whorl height, and triangles represent umbilical diameter. Scales are in millimetres.



- 1906 *Pachydiscus supremus* Petho, p. 88, pl. 5, fig. 1a, b.  
 1908 *Pachydiscus colligatus* van Binkhorst; de Grossouvre, p. 28 *pars*, pl. 4, fig. 3a, b; pl. 5, fig. 1a-c; ?pl. 4, figs. 1a, b, 2; pl. 6, fig. 1a-c.  
 1938 *Parapachydiscus colligatus* van Binkhorst; Collignon, p. 30, pl. 5, fig. 1, 1a.  
 1938 *Parapachydiscus fresvillensis* Seunes; Collignon, p. 57, pl. 7, figs. 4, 4a, b, 5.  
 1955a *Pachydiscus* sp. aff. *colligatus* van Binkhorst; Collignon, p. 74, pl. 26, fig. 2, 2a, 2b.  
 1969 *Pachydiscus colligatus fresvillensis* Seunes; Atabekian and Akopian, p. 13, pl. 6, fig. 1a-b.  
 1971 *Pachydiscus fresvillensis* Seunes; Collignon, p. 30, pl. 652, fig. 2408.  
 1971 *Pachydiscus colligatus* van Binkhorst; Collignon, p. 31, pl. 653, pl. 654, fig. 2409.

*Material.* Thirty specimens, localities 4, 5, 7, 10-12, 15, 16, 18, 19, 23, and 26.

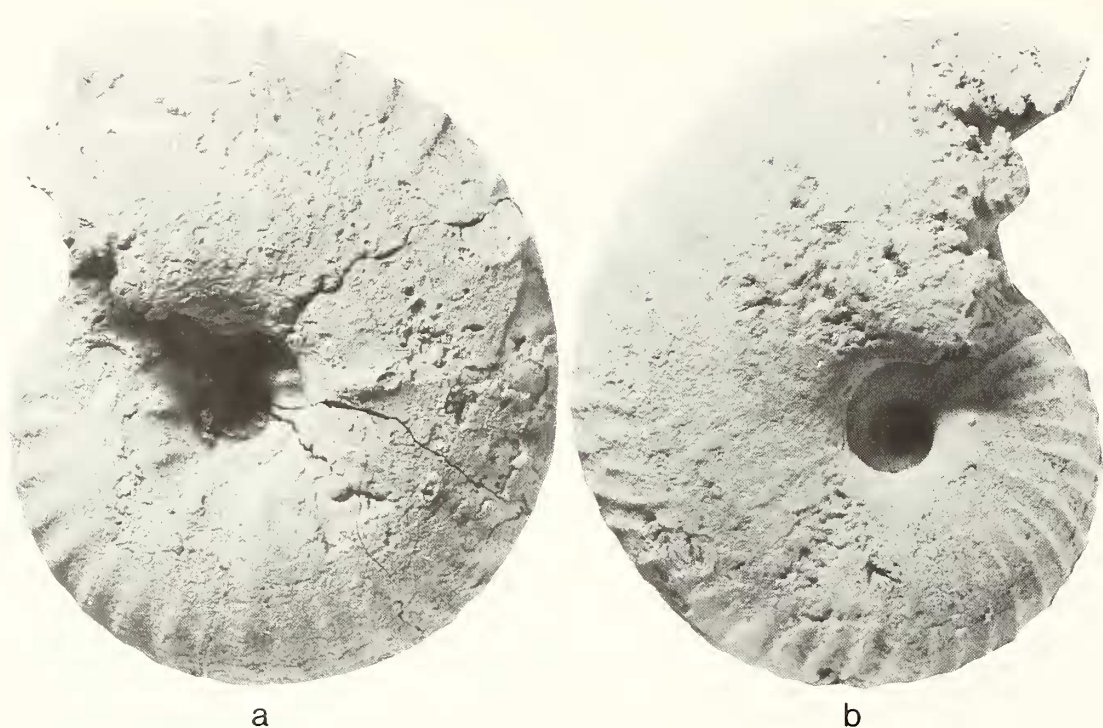
*Description.* Shell involute with the umbilicus measuring 15-21% of the shell diameter. Early whorls are depressed with strongly convex flanks and a broadly arched venter; the whorl breadth/whorl height ratio is about 1.4 at a shell diameter of 3 cm declining to about 1.2 at a shell diameter of 6 cm. At growth stages exceeding about 12.5 cm the whorl profile becomes compressed, the flanks gently convex and slightly convergent, and the venter more narrowly rounded. At its base, the umbilical wall is slightly overhanging. Maximum whorl breadth lies on the dorsal flanks for all stages of ontogeny. Early growth stages, up to a shell diameter of 6 cm, have nine to eleven umbilical bullae per whorl each giving rise to one or two ribs with an equal number of intercalatories beginning from the dorsal flanks so that there are some thirty ribs per whorl. At first they are thin and weak, especially across the venter, but they strengthen progressively with growth. Some can be followed as a faint rursiradial trace on the umbilical wall; they are rectiradial across the flanks but curve forward at the margin of the venter across which they are gently projected. Later growth stages, at shell diameters of 60-120 mm, have eight to nine umbilical bullae each giving rise to one to two ribs with one to three intercalatories beginning from the dorsal flanks to make thirty-seven to forty-two ribs per whorl. Ribs are equally strong on the flanks and venter and correspond in shape to those of earlier volutions. At a shell diameter of about 120 mm, umbilical bullae disappear and ribs become confined to the ventral flanks and venter. Suture typical of the genus except that the umbilical lobe is only slightly retracted on the umbilical shoulder and wall.

*Dimensions.*

	D	H	B	B/H	U	%
WAM 60.761	32.0	15.8	21.8	1.38	5.2	16
NMV P31024	49.5	24.5	30.5	1.24	8.5	17
WAM 81.2388	56.2	26.2	33.5	1.28	11.8	21
WAM 81.2528b	63.0	31.0	36.8	1.19	13.5	21
WAM 81.2707	105.0	53.0	55.5	1.05	19.0	18
WAM 81.2527	123.0	62.0	62.0	1.00	23.5	19
OUM KZ13678	138.0	67.0	69.0	1.02	28.0	20
WAM 81.2623	154.0	80.5	76.0	0.94	25.0	16
NMV P31014	181.0	93.0	84.0	0.90	28.0	15

*Remarks.* The larger Western Australian specimens are inseparable from the holotype of *P. (P.) fresvillensis* Seunes (1890, pl. 1, fig. 1a, b) with which they have been compared by means of a cast (OUM KZ13678) held by the University Museum, Oxford. Ornament of the holotype matches exactly, with the dorsal flanks becoming smooth at a shell diameter of about 12 cm. Its juvenile growth stages are not shown but the whorl profile is depressed (whorl breadth/whorl height ratio of 1.18) at the earliest stage at which it can be measured, corresponding to a shell diameter of some 75 mm.

The identity of *P. (P.) fresvillensis* is much confused in the literature; its relationship to *P. (P.) colligatus* (van Binkhorst, 1861) in particular has been held in question. The type series of *P. (P.) colligatus* (van Binkhorst 1861, pls. 7, 8, 8a) consisted of two complete specimens, measuring nearly 290 mm and 45 mm in diameter, and a number of whorl fragments. Both the complete specimens have effaced ornament with umbilical tubercles lacking and, in common with the fragmentary specimens, an equidimensional whorl profile. Some of the whorl fragments, however, are quite strongly ribbed and possess umbilical tubercles. It may well be that the type series includes more than one species. The interpretation of *P. colligatus* adopted here is based on the two complete specimens which are distinguished from *P. (P.) fresvillensis* by their effaced ribbing, especially that of the



TEXT-FIG. 15. Mature growth stages of *Pachydiscus* species,  $\times 0.5$ . a, *P. (P.) jacquoti australis* subsp. nov., holotype, WAM 80.1004. b, *P. (P.) fresvillensis* Seunes, NMV P31014.

mature volutions, and by the equidimensional rather than strongly depressed whorl profile of the initial growth stages.

*P. colligatus* is here regarded as a senior synonym of *P. ootacodensis* (Stoliczka), 1865, a species which has also remained poorly defined in spite of revision by Kossmat (1898) who segregated one of Stoliczka's type series, a large specimen with distinctive, strong ornament, as *P. grossouvrei* Kossmat. Stoliczka (1865, p. 110) also recognized these species as synonymous but regarded *A. colligatus* van Binkhorst, 1861 as a primary homonym of *A. colligatus* Hoeninghaus, 1830 whereby *ootacodensis* became the valid name. However, *A. colligatus* Hoeninghaus was published merely as part of a list and is a *nomen nudum*, without nomenclatural status. *P. ootacodensis* has been well documented from the Pacific coast of North America by Whiteaves (1895), Usher (1952), and Jones (1963). The North American suite includes specimens with very effaced ornament as well as some, especially juveniles, with stronger ribbing and incipient umbilical tubercles. Jones (1963) segregated the latter as a new species, *P. (P.) hornbyense*, but the suite shows continuous variation and is best regarded as comprising a single, somewhat variable species. As noted by Matsumoto (1959b), the Californian species *P. (P.) stanislausensis* Anderson, 1958 is probably also a synonym of *P. (P.) colligatus*.

#### EXPLANATION OF PLATE 9

Figs. 1–2. *Pachydiscus (Pachydiscus) fresvillensis* Seunes, WAM 81.2527,  $\times 1$ .

Figs. 3–6. *P. (P.) neubergicus dissitus* subsp. nov. 3–4, paratype WAM 80.963,  $\times 1$ . 5–6, paratype WAM 60.54,  $\times 1$ .





HENDERSON and McNAMARA, *Pachydiscus* (*Pachydiscus*)



(= *P. ootacodensis*). All specimens of this assemblage are readily distinguished from *P. (P.) fresvillensis* by virtue of effaced ornament and the juvenile growth stages which are not depressed. The large specimen with strong, mature ribbing figured by Stoliczka (1865, pl. 56, fig. 1) appears to be an exception but the figure is composite, the ribs having been taken from another, and otherwise unfigured, specimen whose specific identity is questionable.

*P. (P.) colligatus* and its synonyms and *P. (P.) fresvillensis* have commonly been confused with two other species, *P. (P.) epiplectus* Redtenbacher, 1873 and *P. (P.) subrobustus* Seunes, 1890. Both of these taxa have ornament of comparable style and strength to that of *P. (P.) fresvillensis* but their initial volutions differ in not being strongly depressed. In addition, the pre-adult ribbing of *P. (P.) epiplectus* is more closely spaced (some twenty-eight per half whorl). De Grossouvre (1894) regarded *colligatus*, *epiplectus*, and *fresvillensis* as synonyms. In the interpretation preferred here, one of his figured specimens (pl. 24, figs. 1, 3) probably represents *P. (P.) subrobustus* whereas the other (pl. 33, figs. 1, 2) represents *P. (P.) epiplectus*. Armenian specimens figured by Mikhailov (1951, pl. 5, fig. 28; pl. 6, fig. 33) as *P. (P.) colligatus* and *P. (P.) colligatus* var. *epiplectus* respectively are here regarded as *P. (P.) epiplectus*. *P. (P.) haueri* Collignon (1955a, p. 75), established for *P. (P.) neubergicus* von Hauer *pars* (1858, pl. 3, figs. 1, 2), is allied to *P. (P.) neubergicus* but distinguished by its ribs which are not projected on the venter. The Armenian specimen figured by Atabekian and Akopian (1969, pl. 8, fig. 1) as *P. haueri haueri* is in fact *P. (P.) epiplectus*. *P. (P.) colligatus* (s.s.) and *P. colligatus michailovi* of Atabekian and Akopian (1969), like *P. colligatus latiumbolicatus* of Błasziewicz (1980), are too strongly ribbed for reference to that species and better considered as *P. subrobustus* Seunes.

Part of the suite figured by de Grossouvre (1908) as *P. colligatus*, certainly the originals of his pl. 4, fig. 2a, b and pl. 5, fig. 1a-c, show the distinctive depressed initial volutions and are typical *P. fresvillensis*. The small specimen illustrated by Stoliczka (1865, pl. 63, fig. 2, 2a) as *P. arrialoorensis* (Stoliczka) is unrelated to the remainder of the type series of that species but indistinguishable from Western Australian *P. fresvillensis* of the same size. *P. supremus* Petho, 1906 also joins the synonymy; it is based on a large Yugoslavian specimen which is very like the largest of the Western Australian suite. All the Madagascan specimens referred by Collignon (1938, 1955a, 1971) to *P. colligatus* are quite strongly ribbed and appear to possess depressed early volutions. They are also grouped in *P. fresvillensis*. The Chilean *P. quiriquinae* Steinmann, 1895, known only from a single, very large specimen, may perhaps represent *P. fresvillensis* but appears to be distinct by virtue of its very weak mature ornament.

The distribution of *P. fresvillensis* embraces eastern and western Europe, Madagascar, southern India, and Western Australia and its established range is late Campanian (*Bostrychoceras polyplocum* Zone) to Maastrichtian.

#### AGE OF THE MIRIA FORMATION

In order to assign an age to the Miria Formation on the basis of its ammonite fauna, it is necessary to review current knowledge of ammonites from the type Maastrichtian and correlative sequences in northern Europe.

Ammonites from the type Maastrichtian of Limburg are poorly known. The classic descriptions of van Binkhorst (1861) and de Grossouvre (1908) were based on small collections of generally poor preservation which have not subsequently been revised. The assemblage they described comprises: *Anagaudryceras* sp., *Sphenodiscus binckhorsti* Bohm, *Pachydiscus* (*Pachydiscus*) *colligatus* (van Binkhorst), *P. (P.) fresvillensis* Seunes, *P. (P.) gollevillensis* (d'Orbigny), *Baculites* spp., *Eubaculites* sp., *Hoploscapites constrictus* (Sowerby), *Diplomoceras cylindraceum* (Defrance), and *Glyptoxoceras* sp. Of these, *S. binckhorsti* is known to occur in the highest member of the Maastricht Formation, the Meersen Chalk (Felder *et al.* 1980), whereas several of the other taxa, including de Grossouvre's (1908) *P. (P.) neubergicus* (von Hauer), were recorded from the older Kunraed Limestone. A twofold ammonite zonation of the standard Maastrichtian Stage with an upper zone of *Sphenodiscus* sp. and a lower zone of *P. (P.) neubergicus*, presumably based on these data, has been adopted by many workers (Spath 1926; Arkell, Kummel and Wright 1957; Kennedy and Cobban 1976; Wiedmann 1979). However, no detailed biostratigraphic data for ammonites in the type Maastrichtian is available. Furthermore, de Grossouvre's (1908) record of *P. (P.) neubergicus* is erroneous. The specimens he referred to this species display a nearly equidimensional whorl profile and probably represent *P. (P.) jacquoti*.

A fourfold belemnite zonation, widely represented throughout northern Europe, has allowed the recognition of the Maastrichtian Stage in several other sequences for which data on the ranges of ammonites are now available. Birkelund (1979) summarized the range data for ammonites in the white chalk of Denmark and later (Birkelund 1982) detailed the biostratigraphy of ammonites in a Maastrichtian chalk quarry at Hemmoor, north-western Germany. The most comprehensive, controlled biostratigraphic zonation is that of Blaszkiewicz (1980), based on the sequence and faunas of the middle Vistula River valley, Poland.

Other general descriptions of Maastrichtian ammonite faunas which make no contribution to a detailed zonation are available for France (d'Orbigny 1840–1842; Seunes 1890–1891; de Grossouvre 1894; see Sornay 1959) and Germany–Austria (Schlüter 1871–1876; Redtenbacher 1873; Thiedig and Wiedmann 1976; see Wiedmann 1979).

A number of conclusions may be reached concerning current knowledge of Maastrichtian ammonite faunas and biostratigraphy in north-western Europe:

1. The assemblage contains a number of distinctive species whose ranges appear to be restricted to the Maastrichtian. In addition to those listed above for the type sequence, these include *Phylloceras* (*Neophylloceras*), *Desmophyllites*, *Saghalinites wrighti* Birkelund, authentic *Pachydiscus* (*P.*) *neubergicus* (von Hauer), *P.* (*P.*) *jacquoti* Seunes, *Pseudokosmaticeras tercense* (Seunes), *Brahmaites* (*Anabrahmaites*) *haugi* (Seunes), *H. tenuistriatus* (Kner), *Acanthoscaphites varians* (Lopuski), *Neancyloceras*, *Nostoceras*, and perhaps *Phylloptychoceras*.

2. Of the genera, only *Sphenodiscus*, *Brahmaites* (*Anabrahmaites*), and *Eubaculites* are not known to range into the Campanian. *Diplomoceras* may also be a restricted Maastrichtian element but the lower limit of its range is open to question.

3. As noted by Birkelund (1982), marked discrepancies occur between species ranges in those sequences for which biostratigraphic detail is known, precluding the recognition of useful zones within the Maastrichtian until a larger body of data is available.

4. Most of the species are endemic to northern Europe, except for those of *Pachydiscus* (*Pachydiscus*) which are widely distributed. The latter, together with the genera *Eubaculites*, *Sphenodiscus*, and *Brahmaites*, offer the best prospects of correlating other Maastrichtian sequences with those of northern Europe.

Direct correlation of the ammonite fauna from the Miria Formation with that of Maastrichtian age in northern Europe is afforded by the shared species of *Pachydiscus* (*Pachydiscus*), *P.* (*P.*) *neubergicus*, *jacquoti*, and *fresvillensis*. Heteromorphs from the Miria Formation we will fully revise elsewhere. We list *Baculites*, *Eubaculites*, *Glyptoxoceras*, and *Diplomoceras* and regard all the new genera proposed by Brunnschweiler (1966) as synonyms. *Nostoceras*, recorded by Brunnschweiler (1966) as from the Miria Formation, we believe to be from the uppermost interval of the underlying Korojon Calcarene. All four heteromorph genera are also represented in the Maastrichtian fauna of northern Europe. Other shared elements, *Phylloceras* (*Neophylloceras*), *Anagaudryceras*, and *Desmophyllites*, are all long-ranging forms.

The fauna of the Miria Formation is closely allied to that of the Maastrichtian Valudayur zone of Pondicherry, southern India, described by Forbes (1846), Stoliczka (1863–1866), and Kossmat (1895, 1897a, 1898) and provided with a biostratigraphic framework by Kossmat (1897b). All the Miria Formation genera, with the exception of the kossmaticeratids other than *Brahmaites*, are shared as are the species. *P.* (*N.*) *surya* (Forbes), *Partschiceras* (*Phyllopachyceras*) *forbesianum* (d'Orbigny), *Gaudryceras kayei* (Forbes), *Pseudophyllites indra* (Forbes), *D. diphyllodes* (Forbes), *Pachydiscus* (*P.*) *neubergicus* (von Hauer (= *A. christina* Forbes) and *E. cf. vagina* (Forbes). The assemblage from that horizon of the Ariyalur Stage, Trichinopoly, southern India, which crops out at Ootacod and contains *A. subtilineatum* (Kossmat), *Gunnarites kalika* Stoliczka, *Brahmaites* (*Brahmaites*) *cf. kossmati* sp. nov. and *Eubaculites* (see Stoliczka, op. cit., Kossmat op. cit.) is also correlative with the Miria Formation, as are the faunas from Madagascar (see Besairie 1972) and south-eastern Africa (see Kennedy and Klinger 1975) which have been assigned a Maastrichtian age.

The Maastrichtian age assigned to the ammonites herein is wholly in agreement with data from Foraminifera. Edgell (1957) assigned a Maastrichtian age to the Miria Formation on the basis of contained *Globotruncana contusa* (Cushman). He recognized the Campanian–Maastrichtian boundary within the underlying Korojon Calcarene, the upper part of which contains benthic Foraminifera typical of the Maastrichtian while the lower part has *G. arca* (Cushman) and other typical Campanian elements. Investigations by Belford (1958) into foraminiferal biostratigraphy of the Miria Formation and underlying units realized the same conclusion. Brunnschweiler (1966) rejected the age assignments of these workers. He considered the kossmaticeratid taxa, with the exception of *Brahmaites*, to be restricted to the lower part of the Miria Marl and to indicate a late Campanian age whereas the upper part of the formation contained a different assemblage and is of Maastrichtian age.

Our investigations do not support Brunnschweiler's view. Most of the ammonites from the Miria Formation are from float and *in situ* specimens are uncommon. To evaluate the possibility of an age difference between various elements of the assemblage, matrix samples from specimens of *Pseudophyllites indra*, *D. diphyloides*, *Gunnarites kalika*, *Maorites densicostatus*, *Pachydiscus* (*P.*) *jacquoti australis* and *P. (P.) fresvillensis* were processed for Foraminifera. Determinations by Dr. M. B. Hart (pers. comm.) have shown that all the samples contain a Maastrichtian assemblage typified by *Globotruncana gansseri* (s.l.), *G. contusa*, *G. arca*, and *Rugoglobigerina rugosa*.

In addition, we have examined sections of the Miria Formation exposed at localities 15–17, 19–21, and 23–25. All sections display the same sequence: an upper portion (0.5–0.75 m) with abundant ammonites and a lower portion (1–2 m) in which ammonites are uncommon to rare. The kossmaticeratids *Gunnarites kalika*, *G. raggatti*, *M. densicostatus*, *Grossouvrites genuatus*, *Kossmaticeras* (*Natalites*) *brunnschwieleri* and *K. (N.)* sp. all occur in the upper portion. The few taxa we have determined from the lower portion, *Phylloceras* (*Neophylloceras*) *surya*, *Gaudryceras kayei*, *Pseudophyllites indra*, *Pachydiscus* (*P.*) *jacquoti australis*, and *Gunnarites kalika*, all have ranges extending into the upper portion.

Nor are there significant differences between collections from different localities of the Miria Formation as suggested by Spath (1941), even though collections have been made at intervals over a strike length of some 80 km.

Kossmaticeratids comprise more than a third of the Miria Formation's non-heteromorph ammonite assemblage and include representatives of *Gunnarites*, *Maorites*, *Kossmaticeras* (*Natalites*), *Neograhamites*, and *Grossouvrites* which have all previously been assigned a Campanian age. It is now apparent that marked late Cretaceous biogeographic provincialism (see Henderson 1970), rather than a temporal pattern, is responsible for the dominance of kossmaticeratid taxa in late Cretaceous ammonite assemblages from New Zealand, Patagonia, and the Antarctic Peninsula.

It may be that the ranges of *Neograhamites*, *G. genuatus* (Huppé), and *M. densicostatus* (Kilian and Reboul) are restricted to the Maastrichtian. Part or all of the Snow Hill Island Series of the Antarctic Peninsula which contains these taxa may be of Maastrichtian age. Other elements shared by the Snow Hill Island Series with the Maastrichtian Valudayur zone of Pondicherry, India, and the Miria Formation, such as *Kitchinites*, *Pachydiscus* (*Pachydiscus*) closely allied to *gollevilleusis*, *Diplonoceras*, and *Polyptychoceras* lend support to such a view.

*Acknowledgements.* We thank Dr. M. B. Hart for determinations of foraminiferal samples and Drs. T. A. Darragh and P. A. Jell (National Museum of Victoria) and Mr. D. Rhodes (University of Western Australia) for access to collections under their charge. Dr. T. A. Darragh and Mr. G. W. Kendrick provided considerable assistance in collecting the fauna. The paper could not have been completed without the generous provision of facilities for R.A.H. at the University Museum, Oxford, arranged by Dr. W. J. Kennedy who is also to be thanked for many productive discussions. Access to collections in the British Museum (Natural History) was arranged by Dr. M. K. Howarth and Mr. D. Phillips. The research was supported by the Australian Research Grants Scheme during 1982–1983.

## REFERENCES

- ANDERSON, F. M. 1958. Upper Cretaceous of the Pacific Coast. *Mem. geol. Soc. Am.* **71**, 378 pp.
- ARKELL, W. J., KUMMEL, B., MILLER, A. K. and WRIGHT, C. W. 1957. Morphological terms applied to Ammonoidea. In MOORE, R. C. (ed.). *Treatise on invertebrate paleontology, part L, Mollusca 4, Cephalopoda, Ammonoidea*, 3–6. Geol. Soc. Amer. and Univ. Kansas Press, New York and Lawrence.
- and WRIGHT, C. W. 1957. Mesozoic Ammonoidea In MOORE, R. C. (ed.). *Ibid.* 80–465.
- ATABEKIAN, A. A. and AKOPIAN, V. T. 1969. Late Cretaceous ammonites of the Armenian SSR (Pachydiscidae). *Proc. Armenian Acad. Sci., Earth Sci.* **6**, 3–20. [In Russian.]
- 1970. Late Cretaceous ammonites of the Armenian SSR (Pachydiscidae, Kossmaticeratidae and Scaphitidae) *Ibid.* **5**, 31–42. [In Russian.]
- BÉ, A. W. H. 1977. An ecological, zoogeographic and taxonomic review of Recent planktonic Foraminifera. In RAMSAY, A. T. S. (ed.). *Oceanic micropalaeontology*, **1**, 1–88. Academic Press, London.
- BELFORD, D. J. 1958. Stratigraphy and micropalaeontology of the Upper Cretaceous of Western Australia. *Geol. Rdsch.* **47**, 629–647.
- BESAIRIE, H. 1972. Géologie de Madagascar. I. Les terrains sédimentaires. *Annls géol. Serv. Mines Madagascar*, **35**, 463 pp.
- BINKHORST VAN DEN BINKHORST, J. T. 1861. *Monographie des gastropodes et des céphalopodes de la Craie*



- Supérieure du Limbourg, suivie d'une description de quelques espèces de crustacés du même dépôt crétacé*, 127 pp. Maastricht.
- BIRKELUND, T. 1965. Ammonites from the Upper Cretaceous of West Greenland. *Medd. Gronland*, **179** (7), 192 pp.
- 1979. The last Maastrichtian ammonites. In BIRKELUND, T. and BROMLEY, R. G. (eds.). *Cretaceous-Tertiary boundary events symposium*, 51–57. Copenhagen.
- 1982. Maastrichtian ammonites from Hemmoor, Hiederelbe (NW Germany). *Geol. Jb.* **A61**, 13–33.
- BLASCO, G., DE NULLO, F. and PROSPERIO, C. 1980. Santoniano-Campaniano: estratigrafia y contenido ammonífero. Cuenca Austral. *Asoc. geol. Argent. Revta*, **35**, 467–493.
- BLASZKIEWICZ, A. 1980. Campanian and Maastrichtian ammonites of the middle Vistula River Valley, Poland. A stratigraphic paleontological study. *Pol. Inst. Geol. Pr.*, **92**, 63 pp.
- BÖHM, J. 1891. Die Kreidebildungen des Furbergs u. Salzbergs bei Siesdorf in Ober-Bayern. *Palaeontographica*, **38**, 1–106.
- BREISTROFFER, M. 1947. Sur les zones d'Ammonites dans l'Albien de France et d'Angleterre. *Trav. Lab. géol. Grenoble*, **26**, 88 pp.
- BRUNNSCHWEILER, R. O. 1966. Upper Cretaceous ammonites from the Carnarvon Basin of Western Australia. I. The heteromorph Lytoceratina. *Bull. Bur. Miner. Resour. Geol. Geophys. Aust.* **58**, 58 pp.
- COLLIGNON, M. 1931. Faunes Sémoniennes du nord et de l'ouest et du sud de Madagascar. *Annls géol. Serv. Mines Madagascar*, **1**, 66 pp.
- 1938. Ammonites Campaniennes et Maastrichtiennes de l'Ouest et du Sud de Madagascar. *Ibid.* **9**, 65 pp.
- 1954. Ammonites néocrétacées du Ménabe (Madagascar). III, Les Kossmaticeratidae. *Trav. Bur. géol. Madagascar*, **63**, 59 pp.
- 1955a. Ammonites néocrétacées du Ménabe (Madagascar). II, Les Pachydiscidae. *Annls géol. Serv. Mines Madagascar*, **21**, 98 pp.
- 1955b. Ammonites néocrétacées du Ménabe (Madagascar). III, Les Kossmaticeratidae. *Ibid.* **22**, 52 pp.
- 1956. Ammonites néocrétacées du Ménabe (Madagascar). IV, Les Phylloceratidae. V, Les Gaudryceratidae. VI, Les Tetragonitidae. *Ibid.* **23**, 107 pp.
- 1961. Ammonites néocrétacées du Ménabe (Madagascar), VII, Les Desmoceratidae. *Ibid.* **31**, 115 pp.
- 1962. *Atlas des fossiles caractéristiques de Madagascar (Ammonites)*. VIII (Berriasien, Valanginien, Hauteriviien, Barremien), 96 pp. Service Géologique, Tananarive.
- 1966. *Atlas des fossiles caractéristiques de Madagascar (Ammonites)*. XIV (Santonian), 134 pp. Service Géologique, Tananarive.
- 1969. *Atlas des fossiles caractéristiques de Madagascar (Ammonites)*. XV (Campanien Inférieur), 216 pp. Service Géologique, Tananarive.
- 1971. *Atlas des fossiles caractéristiques de Madagascar*. XVII (Maastrichtien), 44 pp. Service Géologique, Tananarive.
- 1977. Ammonites néocrétacées de la Nouvelle-Calédonie. *Bull. Bur. Rech. Min. Géol., sect. 4*, **1** (1977), 7–36.
- CONDIT, D. D. 1935. Oil possibilities in North-West District, Western Australia. *Econ. Geol.* **30**, 860–878.
- CONDON, M. A., JOHNSTONE, D., PRICHARD, C. E. and JOHNSTONE, M. H. 1956. The Giralia and Marilla Anticlines, North-West Division, Western Australia. *Bull. Bur. Miner. Resour. Geol. Geophys. Aust.* **25**, 86 pp.
- COOPER, M. R. 1981. Revision of the late Valanginian Cephalopoda from the Sundays River Formation of South Africa, with special reference to the genus *Olcostephanus*. *Ann. S. Afr. Mus.* **83**, 147–366.
- DRUSHCHITS, V. V. 1956. *Lower Cretaceous ammonites of the Crimea and northern Caucasus (Lithoceratidae, Tetragonitidae, and Phylloceratidae)*, 150 pp. Izdatel's tov Moskovskogo Gosudarstvennogo Universiteta. [In Russian.]
- EDGELL, H. S. 1957. The genus *Globotruncana* in Western Australia. *Micropaleontology*, **3**, 101–122.
- FELDER, P. J., FELDER, W. M. and BROMLEY, R. G. 1980. The type area of the Maastrichtian Stage. In BIRKELUND, T. and BROMLEY, R. G. (eds.). *The Upper Cretaceous and Danian of NW Europe*, 118–137. *Int. geol. Congr.* **26**, Paris.
- FORBES, E. 1846. Report on the fossil invertebrates from southern India, collected by Mr. Kaye and Mr. Cunliffe. *Trans. geol. Soc. Lond.* **7**, 97–174.
- FRITSCH, A. and KAFKA, J. 1887. *Die Crustaceen der böhmischen Kreideformation*, 53 pp. Selbstverlag, Prague.
- FUCINI, A. 1920. Fossili domeriani dei dintorni di Taormina. *Palaeontogr. Ital.* **25**, 75–116.
- GEYER, G. 1893. Die Mittelliasischen Cephalopoden—Fauna des Hinter-Schafberges in Oberösterreich. *Abh. geol. Bundesanst., Wien*, **15** (4), 1–76.
- GLENISTER, B. F., MILLER, A. K. and FURNISH, W. M. 1956. Upper Cretaceous and early Tertiary nautiloids from Western Australia. *J. Paleont.* **30**, 492–503.

- GROSSOUVRE, A. DE 1894. Recherches sur la Craie supérieure. 2. Paléontologie. Les ammonites de la Craie supérieure. *Mem. Serv. Carte géol. det. Fr.* 264 pp., atlas of 39 plates. Paris.
- 1908. Description des ammonitides du Crétacé supérieur du Limbourg belge et hollandais et de Hainault. *Mém. Mus. r. Hist. nat. Belg.* **4**, 1–39.
- HAUER, F. VON. 1858. Über die Cephalopoden der Gosauschichten. *Beitr. Palaeontogr. Öst.* **1**, 7–14.
- HENDERSON, R. A. 1970. Ammonoidea from the Mata Series (Santonian?–Maastrichtian) of New Zealand. *Spec. Pap. Palaeont.* **6**, 82 pp.
- 1984. A muscle attachment proposal for septal function in Mesozoic ammonites. *Palaeontology*, **27**, 461–486.
- and KENNEDY, W. J. (in press). *Ammonites chrishna* Forbes, 1846 (Mollusca): proposed suppression of a specific name. *Bull. Zool. Nomen*.
- HOENINGHAUS, F. W. 1830. Versuch einer geognostischen Eintheilung seiner Versteinerung-Sammlung. Zweiter Theil. *Jb. Min. Geognosie Geol. Petrefaktenkund*, **1**, 446–467.
- HOWARTH, M. K. 1958. Upper Jurassic and Cretaceous faunas of Alexander Land and Graham Land. *Scient. Rep. Falkld Isl. Depend. Surv.* **21**, 16 pp.
- 1965. Cretaceous ammonites and nautiloids from Angola. *Bull. Br. Mus. Nat. Hist. Geol.* **10**, 337–412.
- 1966. Ammonites from the Upper Cretaceous of the James Ross Island Group. *Bull. Br. antarct. Surv.* **10**, 55–69.
- HÜNICKEN, M. 1965. Algunos cefalopodos supracretácicos del Rio Turbio (Santa Cruz) *Fac. Cienc. Univ. Nac. Cordoba, ser. Cienc. Nat.* **52**, 49–80.
- HUPPÉ, L. H. 1854. In GAY, R. Fauna chilena. *Hist. Fis. Polit. Chile, Zool.* **8**, 7–54.
- HYATT, A. 1900. Cephalopoda. In ZITTEL, K. A. VON (translated by EASTMAN, C. R.), *Textbook of palaeontology*, 1, 502–604, London.
- JONES, D. L. 1963. Upper Cretaceous (Campanian–Maestrichtian) ammonites from Southern Alaska. *Prof. Pap. U.S. geol. Surv.* **432**, 53 pp.
- KENNEDY, W. J. and COBBAN, W. A. 1976. Aspects of ammonite biology, biogeography and biostratigraphy. *Spec. Pap. Palaeont.* **17**, 94 pp.
- and KLINGER, H. C. 1975. Cretaceous faunas from Zululand and Natal, South Africa. Introduction, stratigraphy. *Bull. Br. Mus. Nat. Hist. Geol.* **25**, 263–315.
- 1977a. Cretaceous faunas from Zululand and Natal, South Africa. The ammonite family Phylloceratidae. *Ibid.* **27**, 349–380.
- 1977b. Cretaceous faunas from Zululand and Natal, South Africa. The ammonite family Tetragonitidae Hyatt, 1900. *Ann. S. Afr. Mus.* **73**, 149–197.
- 1979. Cretaceous faunas from Zululand and Natal, South Africa. The ammonite family Gaudryceratidae Spath 1927. *Bull. Br. Mus. Nat. Hist. Geol.* **31**, 121–174.
- (in press). Cretaceous faunas from Zululand and Natal, South Africa. The ammonite family Kossmaticeratidae Spath, 1922. *Ann. S. Afr. Mus.*
- KILIAN, W. and REBOUL, P. 1909. Les céphalopodes néocrétacés des îles Seymour et Snow Hill. *Wiss. Ergebn. schwed. Sudpolarexped.* **6**, 1–75.
- KITCHIN, F. L. 1908. The invertebrate fauna and palaeontological relationships of the Uitenhage Series. *Ibid.* **7**, 21–225.
- KLINGER, H. C., KAUFFMAN, E. G. and KENNEDY, W. J. 1980. Upper Cretaceous ammonites and inoceramids from the off-shore Alphonse Group of South Africa. *Ann. S. Afr. Mus.* **82**, 293–320.
- KOSSMAT, F. 1895. Untersuchungen über die südindische Kreideformation. Erster Theil. *Beitr. Palaeont. Geol. Öst.-Ung.* **9**, 97–203.
- 1897a. Untersuchungen über die südindische Kreideformation. Zweiter Theil. *Ibid.* **11**, 1–46.
- 1897b. The Cretaceous deposits of Pondicherry. *Rec. geol. Surv. India*, **30**, 51–110.
- 1898. Untersuchungen über die südindische Kreideformation. Dritter Theil. *Beitr. Palaeont. Geol. Öst.-Ung.* **11**, 89–152.
- KOVACS, L. 1942. Monographie der Liassischen Ammoniten des Nordlichen Bakony. *Geologica hung., ser. palaeontologica*, **17**, 1–220.
- KULLMAN, J. and WIEDMANN, J. 1970. Significance of sutures in phylogeny of Ammonoidea. *Paleont. Contrib. Univ. Kansas*, **44**, 32 pp.
- LEANZA, A. F. 1964. Los estratos con 'Baculites' de Elcain (Rio Negro Argentina) y sus relaciones con otros terrenos supracretácicos Argentininos. *Fac. Cienc. Univ. Nac. Cordoba, ser. Cienc. Nat.* **51**, 93–107.
- 1967. Descripción de la fauna de *Placenticerias* de Cretácico Superior de Patagonia Austral con consideraciones acerca de su posición estratigráfica. *Boln. Acad. nac. Cienc. Cordoba*, **46**, 5–28.

- MARSHALL, P. 1926. The Upper Cretaceous ammonites of New Zealand. *Trans. N.Z. Inst.* **56**, 129–210.
- MATSUMOTO, T. 1942. A note on the Japanese Cretaceous ammonites belonging to the Subfamily Desmo-ceratinae. *Proc. imp. Acad. Japan*, **18**, 24–29.
- 1947. A note on the Japanese Pachydiscidae. *Rep. Dep. Geol. Fac. Sci. Kyushu Univ.* **2**, 34–36. [In Japanese.]
- 1954a. Selected Cretaceous leading ammonites from Hokkaido and Saghalien. In MATSUMOTO, T. (ed.). *The Cretaceous system in the Japanese islands*, 243–313. Tokyo.
- 1954b. Family Puzosiidae from Hokkaido and Saghalien. *Mem. Fac. Sci. Kyushu Univ.*, ser. D, **5**, 69–118.
- 1955. Family Kossmaticeratidae from Hokkaido and Saghalien. *Jap. J. Geol. Geogr.* **26**, 115–164.
- 1959a. Cretaceous ammonites from the Upper Chitina Valley, Alaska. *Mem. Fac. Sci. Kyushu Univ.*, ser. D, **8**, 49–90.
- 1959b. Upper Cretaceous ammonites of California. Part II. *Ibid. Spec. Vol.* 1, 172 pp.
- and MOROZUMI, Y. 1980. Late Cretaceous ammonites from the Izumi Mountains, southwest Japan. *Bull. Osaka Mus. Nat. Hist.* **33**, 1–31.
- MAURY, C. J. 1930. O cretaceo da parayhya do norte. *Monogr. Serv. geol. min. Brazil*, **8**, 305 pp.
- MCGOWRAN, B. 1968. Late Cretaceous and early Tertiary correlations in the Indo-Pacific region. *Mem. Geol. Soc. India*, **2**, 335–360.
- 1978. Early Tertiary foraminiferal biostratigraphy in southern Australia: a progress report. *Bull. Bur. Miner. Resour. Geol. Geophys. Aust.* **192**, 83–95.
- MEEK, F. R. 1857. Descriptions of new organic remains from the Cretaceous rocks of Vancouver Island. *Trans. Albany Inst.* **4**, 37–49.
- MIKHAILOV, N. P. 1951. The ammonites of the southern part of the European part of the USSR and their stratigraphic significance. *Trudy Inst. geol. Nauk*, **129**, 143 pp. [In Russian.]
- ORBIGNY, A. d' 1840–1842. *Paléontologie française. Terrains Crétacés I. Céphalopodes*, 662 pp. Paris.
- 1850. *Prodrome de paléontologie stratigraphique universelle des animaux mollusques et rayonnés II*, 427 pp. Paris.
- PACKARD, E. L. 1960. Hypotypes of *Phylloceras onoense* Stanton. *J. Paleont.* **34**, 421–428.
- PAULCKE, W. 1906. Die Cephalopoden der oberen Kreide Südpatagoniens. *Ber. naturf. Ges. Freiberg i. B.* **15**, 167–248.
- PETHO, J. 1906. Die Kreide (Hypersenon) Fauna des Peterwardeiner (Petervarader) Gebirges (Frusca Gora). *Palaeontographica*, **52**, 57–331.
- RAGGATT, H. G. 1936. Geology of the North-west Basin, Western Australia. *J. R. Soc. N.S.W.* **70**, 100–174.
- REDTENBACHER, A. 1873. Die Cephalopoden fauna der Gosauschichten in der nordöstlichen Alpen. *Abh. K.-K. geol. Reichsanst. Vienna*, **5**, 91–140.
- ROMAN, F. 1938. *Les ammonites Jurassiques et Crétacées. Essai de genera*, 554 pp. Masson, Paris.
- SALFELD, H. 1919. Über die Ausgestaltung der Lobenlinie bei Jura- und Kreideammonoideen. *Nachr. Ges. Wiss. Göttingen, Mathematisch-physikalische Klasse*, **3**, 449–467.
- 1924. *Die Bedeutung der Konservativstämme für die Stammesentwicklung der Ammonoideen*, 16 pp. Leipzig.
- SCHLÜTER, C. 1871–1876. Die Cephalopoden der oberen deutschen Kreide. *Palaeontographica*, **21**, 1–24 (1871), **21**, 25–120 (1872), **24**, 1–44 (1876).
- SEUNES, J. 1890. Contributions a l'étude des Céphalopodes du Crétacé supérieur de France. *Mém. Soc. Géol. France, Paléont. Mém.* **2**, 3–7.
- 1891. Contributions a l'étude des Céphalopodes du Crétacé supérieur de France. *Ibid.* 9–22.
- SHIMIZU, S. 1934. Ammonites. In SHIMIZU, S. and OBATA, T. *Cephalopoda*. Iwanami's Lecture Series of Geology and Paleontology, 137 pp. Tokyo. [In Japanese.]
- 1935. The Upper Cretaceous cephalopods of Japan. Part 1. *Shanghai Sci. Inst.*, sect. 2, **2**, 59–226.
- SORNAY, J. 1959. Généralités sur les faunes d'ammonites du crétacé supérieur. IV. Le Maestrichtien. *Comptes rendus du congrès des sociétés savantes de Paris et des Départements. Section des Sciences, sous-section de Géologie, colloque sur le crétacé supérieur Français*, 23–25. Gauthier-Villars, Paris.
- SPATH, L. F. 1921. On upper Cretaceous Ammonoidea from Pondoland. *Ann. Durban Mus.* **3**, 39–57.
- 1922. On the Senonian ammonite fauna of Pondoland. *Trans. R. Soc. S. Afr.* **10**, 113–147.
- 1926. On new ammonites from the English Chalk. *Geol. Mag.* **63**, 77–83.
- 1927. Revision of the Jurassic cephalopod fauna of Kachh (Catch). *Mem. geol. Surv. India, Palaeont. indica*, **9**, (2) 71 pp.
- 1929. Corrections of cephalopod nomenclature. *Naturalist*, **871**, 269–271.
- 1941. On Upper Cretaceous (Maestrichtian) Ammonoidea from Western Australia. *J. Proc. R. Soc. West Aust.* **26**, 41–54.



- SPATH, L. F. 1953. The Upper Cretaceous cephalopod fauna from Graham Land. *Scient. Rep. Falkld Isld Depend. Surv.* **3**, 60 pp.
- STEINMANN, G. 1895. Die Cephalopoden der Quiriquina-Schichten. In STEINMANN, G., DEECKE, W. and MORICKE, W. Das Alter und die Fauna die Quiriquina-Schichten in Chile. *Neues Jb. Miner. Geol. Palaont., Beil. Bd.* **10**, 64-94.
- STOLICZKA, F. 1863-1866. The fossil Cephalopoda of the Cretaceous rocks of southern India. *Mem. geol. Surv. India, Palaeont. indica*, **3**, 41-56 (1863), 57-106 (1864), 107-154 (1865), 155-216 (1866).
- STURANI, C. 1966. Ammonites and stratigraphy of the Bathonian in the Digne-Barrême area (south-eastern France, Dept. Basses-Alpes). *Boll. Soc. Paleont. Italiana*, **5** (1), 1-55.
- THIEDIG, F. and WIEDMANN, J. 1976. Ammoniten und Alter der höheren Kreide (Gosau) des Krappfeldes in Kärnten (Österreich). *Mitt. Geol.-Paläont. Inst. Univ. Hamburg*, **45**, 9-27.
- USHER, J. L. 1952. Ammonite faunas of the Upper Cretaceous of Vancouver Island, British Columbia. *Bull. Geol. Surv. Canada*, **21**, 182 pp.
- VAN HOEPEN, E. C. N. 1920. Description of some Cretaceous ammonites from Pondoland. *Ann. Transv. Mus.* **7**, 142-147.
- 1921. Cretaceous Cephalopoda from Pondoland. *Ibid.* **8**, 1-48.
- WARD, P. D. 1978. Revisions of the stratigraphy and biochronology of the Upper Cretaceous Nanaimo Group, British Columbia and Washington State. *Can. J. Earth Sci.* **15**, 405-423.
- WEDEKIND, R. 1916. Über Lobus, Suturallobus und Inzision. *Centralbl. Miner. Geol. Palaeont.* (1916), 185-195.
- WELLER, S. 1903. The Stokes collection of Antarctic fossils. *J. Geol.* **11**, 413-419.
- WHITEAVES, J. F. 1879. On the fossils of the Cretaceous rocks of Vancouver and adjacent islands in the Strait of Georgia. *Geol. Surv. Canada, Mesozoic Fossils*, **1**, 93-190.
- 1895. On some fossils from the Nanaimo Group of the Vancouver Cretaceous. *Trans. R. Soc. Canada, sect. 4*, **1**, 119-133.
- WIEDMANN, J. 1962a. Die systematische Stellung von *Hypophylloceras* Salfeld. *Neues Jb. Geol. Paläont. Abh.* **115**, 243-256.
- 1962b. Ammoniten aus der vascogotischen Kreide (Nordspanien). I. Phylloceratina Lytoceratina. *Palaeontographica*, **A118**, 119-237.
- 1964. Unterkreide-Ammoniten von Mallorca, 2. Lieferung, Phylloceratina. *Abh. math.-naturw. Kl. Akad. Wiss. Mainz* (1963), 151-264.
- 1969. The heteromorphs and ammonoid extinction. *Biol. Rev.* **44**, 563-620.
- 1979. Die ammoniten der NW-deutschen, Regensburger und Ostalpinen Oberkreide im Vergleich mit den Oberkreidefaunen des westlichen Mediterraengebietes. In WIEDMANN, J. (ed.). *Aspekte der Kreide Europas*, 335-350. E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart.
- and DIENI, I. 1968. Die Kreide Sardinien und ihre Cephalopoden. *Palaeont. Italica*, **64**, 171 pp.
- WRIGHT, C. W. and MATSUMOTO, T. 1954. Some doubtful Cretaceous ammonite genera from Japan and Saghalien. *Mem. Fac. sci. Kyushu Univ., ser. D*, **4**, 107-134.
- YABE and SHIMIZU, S. 1924. A new species of *Bralmaites* from the Upper Cretaceous of S. Saghalin with some remarks on the genus *Bralmaites*. *Jap. J. Geol. Geogr.* **3**, 77-80.
- ZITTEL, K. A. 1884. *Handbuch der Palaeontologie*, 1, Abt. 1, Lief. 3, *Cephalopoda*, 329-522. Munich and Leipzig.

R. A. HENDERSON

Department of Geology  
James Cook University  
Townsville  
Queensland 4811  
Australia

K. J. MCNAMARA

Department of Palaeontology  
Western Australian Museum  
Perth  
Western Australia 6000

Typescript received 2 December 1983

Revised typescript received 11 May 1984